What makes species more vulnerable to environmental change? Passerines as a case study

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by

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Declaration of work carried out

I declare that the work presented in this thesis, which was conducted in part at the Centre for Ecology and Hydrology (Edinburgh) and at the School of Biological Sciences, University of Liverpool, is my own, and has not been accepted in any previous application for a degree. All sources of information have been specifically acknowledged.

This thesis is submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor of Philosophy.

Work in all chapters of this theses is based on data collected by the BTO (British Trust for Ornithology) either as part of the work on the population status of the common birds of the wider UK countryside (Chapter two) or Breeding Bird Atlas I and II (during the years 1968-72 and 1988-91 respectively) (Chapters three to six). Work in Chapter Two involved the use of a phylogenetic tree developed by Dr Gavin Thomas, University of Sheffield. Work in Chapters Three to Six in this thesis also used data produced as part of the FRAME project on pollutant concentrations and deposition carried out at CEH Edinburgh and data on land cover use in Europe produced by the Ecochange project.

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“ It is not the strongest of the species that survives,

nor the most intelligent that survives.

It is the one that is most adaptable to change”

Charles Darwin

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Summary

Environmental change presents the greatest challenges to biodiversity conservation. From climate changes to land cover conversion and pollution effects, global biodiversity faces many threats. Though conservation actions have been put into place to halt the loss of biodiversity, recent studies suggest that conservation actions have largely failed to do this. Hence, understanding the links between species responses, environmental pressures and the role of species characteristics in conferring resilience to these environmental pressures would be fundamental to develop adequate conservation measures.

This thesis focuses on a range of approaches to investigate the impacts of well-known environmental pressures on the passerine community in the UK to try to uncover mechanisms underpinning species responses to environmental change. Furthermore, considering that bird species are currently been used as biodiversity indicators, it would be of great use to identify new venues to measure and monitor species responses to environmental change that would help improve the current set of indicators.

Examining multiple pressures within the same analytical framework was valuable for demonstrating that land cover and pollution drivers are of equivalent importance to climate in structuring bird communities at a broad scale in the UK. Both community and niche studies revealed that winter conditions and pollution were key in structuring passerine communities together with pollution at this broad scale. In terms of colonisation and extinction processes the spatial structure of the species occupancy appeared to have a dominant role in driving the observed dynamics as well as again, climate change in terms of warming winter temperatures.

Throughout this thesis, the above mentioned ecological responses were linked to species ecological traits with the aim of gaining a greater understanding of the mechanisms underpinning species' differential responses to environmental change and identifying those trait groups that may be most vulnerable or most valuable as indicators. A significant group of characteristics that consistently appeared to be linked to species resilience to observed environmental pressures (particularly climate change) was phenological traits. Species with earlier laying dates and/or longer laying periods were associated with increasing population trends, larger colonisation rates and smaller extinction rates.

Also analysis of species niches in relation to environmental pressures not only revealed the dynamic nature of niche parameters, confirming niche evolution and niche tracking in some species but also confirmed their relationship with both species characteristics and current conservation categories.

Finally this study reiterated the fact that relationships between species characteristics and environmental pressures involve complex interactions that significantly affect and transform species responses to environmental pressures. For example the interaction between migratory behaviour and phenological traits (i.e. earlier laying dates and longer laying periods) meant that migrant species were less likely to have declining populations or that warming winter temperatures were associated with increased colonisation for migrants or species with more annual broods were less likely to show extinction in cells with temperature increase.

All these results not only confirm the suitability of birds and particularly passerine species as indicators of environmental use and their potential and importance as part of indices and monitoring programmes but also highlights the importance of updating the next generation of indicators with measurements that can take into account important species characteristics associated with resilience to environmental pressures (i.e. phenological traits).

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Chapter 1 : General Introduction

Environmental change and particularly climate change, presents a major threat to biodiversity conservation and ecosystem function. Though the adoption of the 2010 biodiversity targets in Johannesburgh in 2002 (World Summit on Sustainable Development, 2002) required that some 170 signatory countries develop and implement national biodiversity strategies and action plans, these measures have not been sufficient to address the pressures on biodiversity (CBD, 2010).

In terms of immediate threats to biodiversity, five main ones have been identified by the Convention on Biological Diversity (CBD), these are: climate change, habitat loss and degradation, pollution and nutrient load, overexploitation and unsustainable use of natural resources and invasion of alien species. Considering the importance that changes in the abundance and distribution of species may have on human societies (i.e. shifts in distribution of animal and plant species could severely affect fisheries, wood and crop harvests, recreation opportunities and other multiple ecosystem services) it is fundamental to promote further understanding of biodiversity loss issues and integrate them into broader policies, strategies and programmes (CDB, 2010). A major drawback in terms of policy implementation has been the scientific uncertainty with respect to exact connections between biodiversity, human well-being and ecosystem functioning (Heller & Zavaleta, 2009). Studies aimed at advancing knowledge of the relationships between species, communities and environment, particularly in terms of species responses to multiple, interacting anthropogenic pressures (such as climate change and land use cover change), will greatly help identify and implement more effective conservation and mitigation practices (Root & Schneider, 2006).

1.1 Pressures driving environmental change

Evidence of climate change is mounting both globally and regionally and ecological impacts of these changes are increasingly well documented (Rosenzweig et al., 2007). Many aspects of climate, including temperature and precipitation and their variability, influence characteristics and distributions of both physical and biological systems (Rosenzweig et al., 2007). Temperature is the focus of most studies on the impact of climate change since its anthropogenic signal is easily detected and physiological and biological responses to its changes are often better understood than responses to other parameters (Rosenzweig et al., 2007). Mean temperature and precipitation (including daily maximums and minimums) and their seasonal cycles over relatively large areas show the clearest signals of change in the observed climate (IPCC, 2001, Fig 1.1). In addition, changes in the intensity and frequency of climatic disturbances such as droughts, floods, freezing temperatures, etc., have affected ecosystems in many continents by for example altering species composition or increasing the frequency of pests and disease outbreaks (Gitay et al., 2002).

Recent observed temperature changes indicate an increase of 0.74 ºC in global mean temperature relative to pre-industrial levels (Fig 1.1 blue line). This increase has already produced notable effects in biodiversity. Since temperature is known to present a physiological constraint to most animal and plant species, the observed climate warming has strongly affected their distribution and abundance patterns, many species moving poleward and upward in elevation in the last century (Parmesan & Yohe, 2003; Root et al., 2003; Parry et al., 2007). Phenological changes in populations have also been reported with worldwide advances in the starting times of growing seasons of between 5-20 days on average (Linderholm, 2006). These changes not only represent an direct impact on the affected species but can also have cascading effects on ecosystems by impacting on other species interactions that have

evolved in a synchronised manner (i.e. nesting and food availability or pollinators and fertilization) (CDB, 2010; Walther et al., 2002).

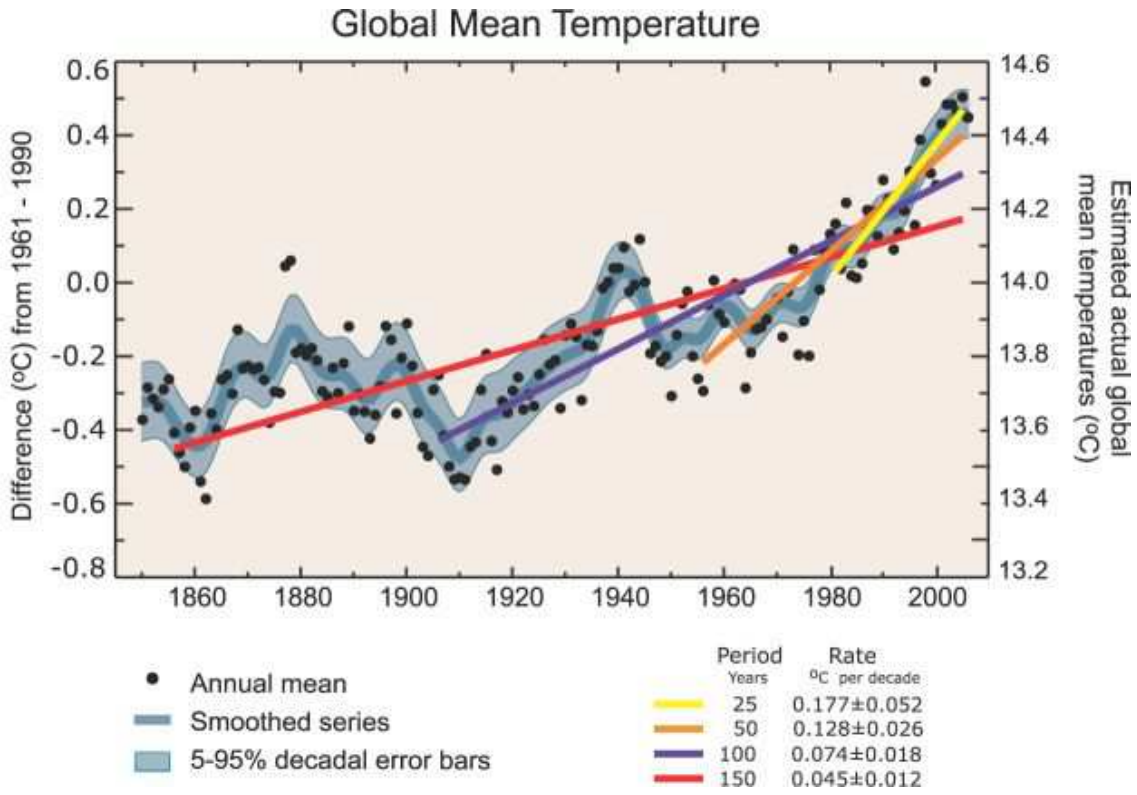
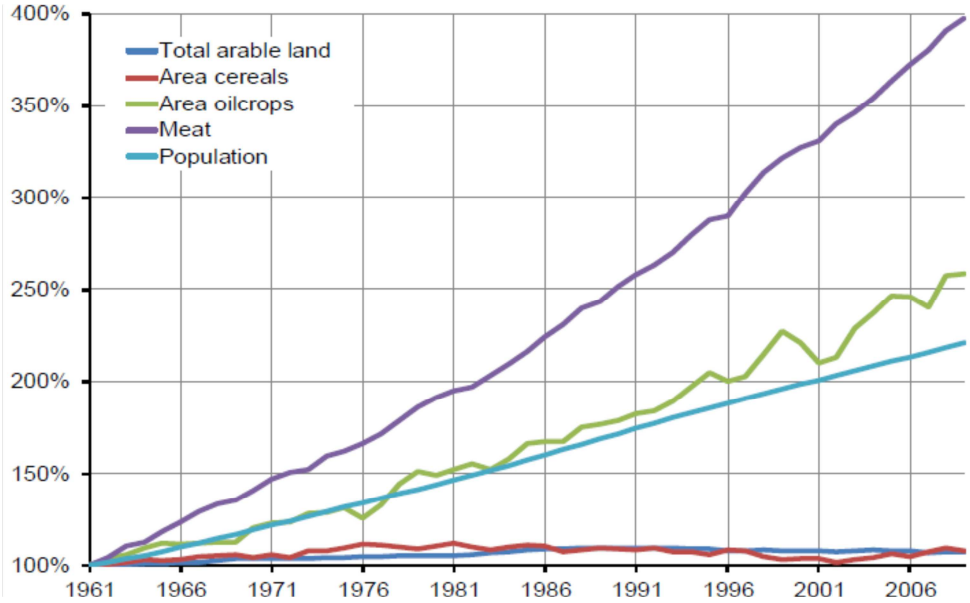


Figure 1.1 Recent temperature increases in global mean temperature (source, IPCC, 2007 (Working Group I. The Physical Science Basis on www.ipcc.ch)). The different coloured bars represent the rate of temperature change observed in different time periods: yellow (25 years), brown (50 years), blue (100 years), red (150 years).

Another major driver of biodiversity and ecosystem change is habitat loss, particularly in the form of land cover/land use change. For much of the 20th century, there has been a significant transformation of habitats; satellite observations have demonstrated that land use change is proceeding at an unprecedented rate (Rindfuss et al., 2004) (Fig 1.2). Particularly, rates of conversion of natural land covers (i.e. grasslands, forests) to agriculture (which accounts now to some 30% of the land globally (CBD, 2010) have had notable negative effects on biodiversity. For example Laliberte & Tylianakis (2010) demonstrated that losses of forested areas in tropical regions lead to

homogenization (i.e. loss of regional richness) of parasitoid-host networks. The IUCN Red Lists also suggest that habitat loss due to agriculture and unsustainable forest management are the greatest source of species extinctions (Jetz et al., 2007; Brooke et al., 2008).

a)



b)

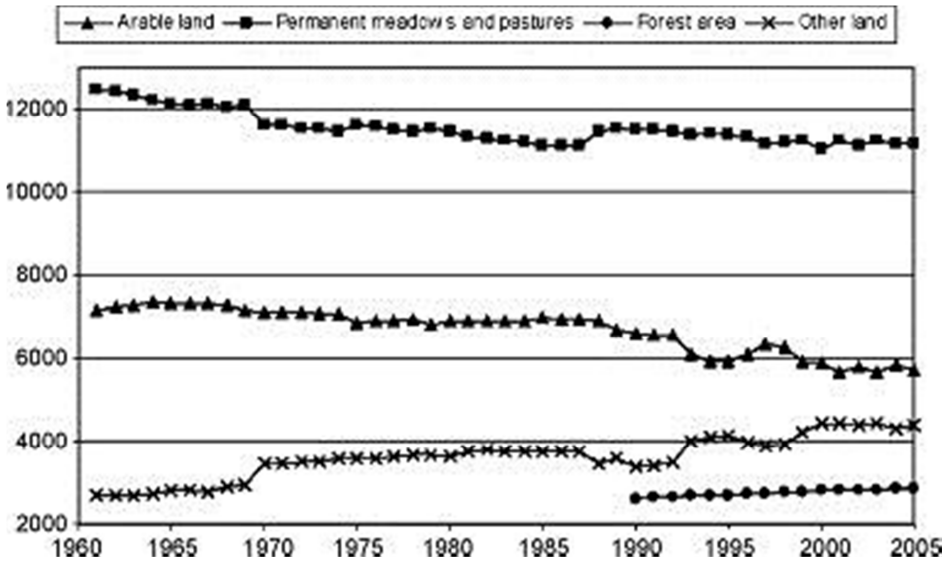


Figure 1.2 a) World agricultural resources and population trends in terms of % change (1961-2006) (source FAOSTAT Agricultural database on www.fao.org); **b) change in UK land use areas (1000ha) for different land use categories (1961-2005)** (from Rounsevell & Reay, 2009).

Another major contributor to biodiversity loss has been pollution and nutrient load. Air pollution and its associated effects, particularly acidification caused by sulphur (SOx) and nitrogen (NOx) deposition, has been a major cause of species loss (CDB, 2010). Nitrogen soil concentrations have also significantly increased since pre-industrial times due to the increased use of fertilizers in agricultural systems (Fig 1.3). Changes in the concentrations of these pollutants have been shown to affect organisms through the acidification of both soils and waters (habitat alteration) or by directly disturbing individuals through physical stress (Jarvis, 1993; Furness, 1993; Graveland, 1998).

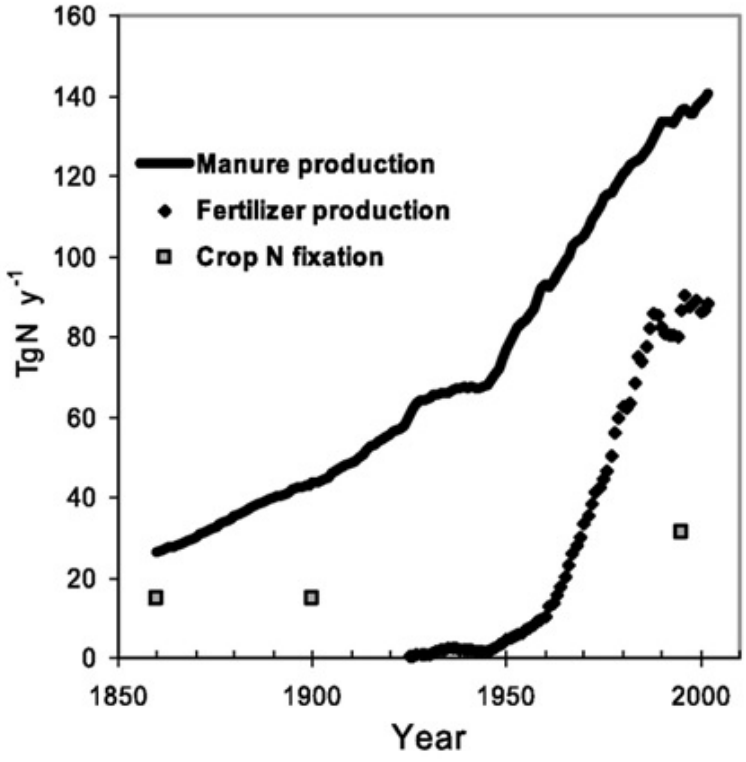


Figure 1.3 Change in global agricultural N cycle since 1850 (source IPCC, 2007 (Working Group I. The Physical Science Basis on www.ipcc.ch)).

Also, is worth mentioning the role of increasing rates of consumption and /or exploitation of biotic resources as the numbers of livestock, timber extraction and other such activities increase the pressure on ecosystems by for example driving land use change (DEFRA, 2006).

The combined pressures of the different extrinsic drivers mentioned above will create an even larger impact on biodiversity and ecosystems compared to their individual effects (Rosenzgweiz et al., 2007; Morecroft et al., 2009). In general, the effects of one driver will exacerbate the impacts of another, for example: the loss of a habitat will reduce the capacity of species to adapt to climate change by reducing their chances of migrating to more suitable conditions, or increased nutrient levels and the presence of invasive species could promote the growth of alien species in comparison to local natives (Chazal & Rounsevell, 2009). For example, Warren et al. (2001) showed that over three quarters of the butterfly species in their study declined as a result of the combined effects of habitat fragmentation and climate change. Hence, it is of vital importance to look at multiple pressures simultaneously when assessing their effect on species and ecosystems to better quantify their impact and interactions and therefore develop efficient conservation and adaptation measures (Helter et al., 2009).

1.2 Species characteristics determining vulnerability to extinction and environmental change. Birds as bioindicators for biodiversity monitoring

As mentioned before, the capacity of species and ecosystems to resist environmental change will be dependent on their ability to adapt to the new conditions or migrate to more suitable habitats. It has been recognized that differences among taxa would be at least partially due to difference in biological traits (Cardillo et al., 2008). In fact, several species characteristics have been linked with species vulnerability to extinction (Purvis et al., 2000; Reynolds et al., 2005; Julliard et al., 2004; Gregory et al., 2005; Cardillo et al., 2005; Salido et al., 2012; Van Turnhout et al., 2010):

i) Species with small populations are more likely to disappear due to demographic stochasticity or slow rates of adaptation,
ii) Endemic species will normally present restricted ranges and small populations and due to the fact that they would have normally evolved in

isolation from other competitor and predator species could be more vulnerable to invasive or alien species,

iii) Species with 'slow' life histories (small litters/clutches, long gestation…) will be less able to compensate for losses due to increased mortality,

iv) Species with large home ranges will be more likely to be affected by land cover changes through habitat loss,

v) Large bodied species have been linked to other extinction prone traits (low reproduction, small population sizes, larger home ranges) which also makes them more susceptible to potential changes in their environment.

vi) Migratory behaviour has also been related to increasing vulnerability to environmental change as species will be less suited to adapt to changes occurring in their breeding grounds as they will lack cues available to resident species through the year.

Ideally, all aspects of the ecosystem should be monitored to quantify and assess their status and responses to the environmental change drivers. However, finite resources and the complexity of natural ecosystems make it practicable to monitor only a small subset of these features (Chambers, 2008).

Therefore, bio-indicators would be species that are particularly sensitive and likely to respond to environmental changes (Lindenmayer & Burgman, 2005). Birds as a group have a range of attributes that makes them extremely useful as indicator species (Padoa-Schioppa et al., 2006; Chambers, 2008; Hvenegaard, 2011):

- They are easy to detect and observe (McNally et al., 2004)
- Their taxonomy is well-known and species are easily identifiable (Gregory et al., 2005)
- Their distribution, biology, ecology and life history are well known compared to other taxa (Gregory et al., 2005).
- Some avian taxa are at the top, or near the top of the food chain, so they are sensitive to changes at lower levels and to environmental

contaminants (Furness et al., 1993; MacNally et al., 2004; Gregory et al., 2005).

- They are of interest or concern to both the public and decision-makers (MacNally et al., 2004; Gregory et al., 2005) which generates strong support for conservation programmes that involve birds and favours volunteer-based monitoring programs reducing costs and increasing the potential scope of monitoring programmes (Silvertown, 2009).
- Survey techniques for birds are relatively simple and capable of capturing information on a multitude of species simultaneously (Hutto, 1998).

Birds have been used as indicator species by government agencies in Europe, Australia and North America (Chambers, 2008; Weber et al., 2008; Gregory & Van Strien, 2010). The Pan-European Common Bird Monitoring Scheme (PECBMS) uses composite indices for common birds to assess the state of biodiversity across Europe, with 148 species of birds recorded in programs over 25 countries (PECBMS 2011, http://www.ebcc.info). In North America, the United States Department of Agriculture Forest Service are required by internal policy to identify and monitor 'management indicator species' (amongst which are birds) within each national forest to determine the impacts of management regimes on forest communities (US Congress Office of Technology Assessment 1992). In Australia, at national and state/territory levels, birds have been used as indicator species for State of the Environment (SoE) reporting (www.environment.gov.au/soe/index/html).

Furthermore, animal groups such as birds demonstrate that bioindicators can be effective tools in communicating information about diversity to the public, policy-makers and governments (Gregory et al., 2003; Gregory & van Strien, 2010). However, the outputs generated by these studies need to be based on reliable and accurate data collection and the links between the bio-indicator species and focal environmental drivers should be clear in order to facilitate

effective, reliable and traceable conservation policy and action plans (Gregory et al., 2003).

1.3 State of UK ecosystems, birds and policy implementation

As a signatory country of the CBD, the UK has regional and global obligation in terms of biodiversity conservation. In order to comply with part of these obligations and also as a need to comply with the Millennium Ecosystem Assessment (MA) and its goals, the UK National Ecosystem Assessment was established in 2005 (UKNAE, 2011, www.uknea.unep-wcmc.org) to "…ensure adequate decisions are taken to guarantee the long-term sustainable delivery of ecosystem services for the benefit of current and future populations in the UK…' (UKNAE, 2011).

In line with the mentioned global environmental pressures discussed earlier the following five factors are identified as major environmental change drivers:

- land use and habitat change,
- pollution and nutrient enrichment,
- overexploitation,
- climate variability and
- change and biological drivers (i.e. invasive alien species).

Land use and land cover change have been key altering forces of the UK environment. As in the case of global ecosystems, a large proportion of the semi-natural vegetation areas in UK was converted to agricultural land from 1940's to 1990's (Robinson & Sutherland, 2002). However, since then there has been a significant decrease in arable land with semi-natural lands such as grassland increasing significantly. Nevertheless, agricultural and arable land types have undergone a simplification and specialization, which may indicate a

more intensified and effective use of the land thanks to increase mechanization and use of fertilizers (Jarvis, 1993; UKNAE, 2011).

In terms of pollution and nutrient enrichment, the impact of these factors has varied significantly in the UK since World War II (UKNAE, 2011). Sulphur deposition was the main cause of acidification of ecosystems during the 1970s though since then there has been a major decline with 90% reductions since that peak (RoTAP, 2010). Meanwhile, nitrogen loads continue to impact ecosystems, mainly through runoff from agricultural land. The application of fertilizers rapidly increased since the 1950s with nitrogen application rates in 1986 almost double those of 1971 (Thomas, 2010).

Rates of consumption and over exploitation have also had notable impacts on UK biodiversity and ecosystems. For example, increasing livestock numbers during the 1950s up to 1980s-1990s meant that, due to grazing pressure, moorlands and mire habitats were transformed to grassland communities (UKNAE, 2011).

Finally the effects of climate change have also been felt. Trends in UK surface air temperature indicate a similar increase in temperature as that observed globally (~0.9ºC) from 1850 until the present day (Fig 1.4). Also precipitation patterns have been reported to have changed with decrease in summer precipitation though the patterns for this variable are less uniform among regions (UKNAE, 2011).

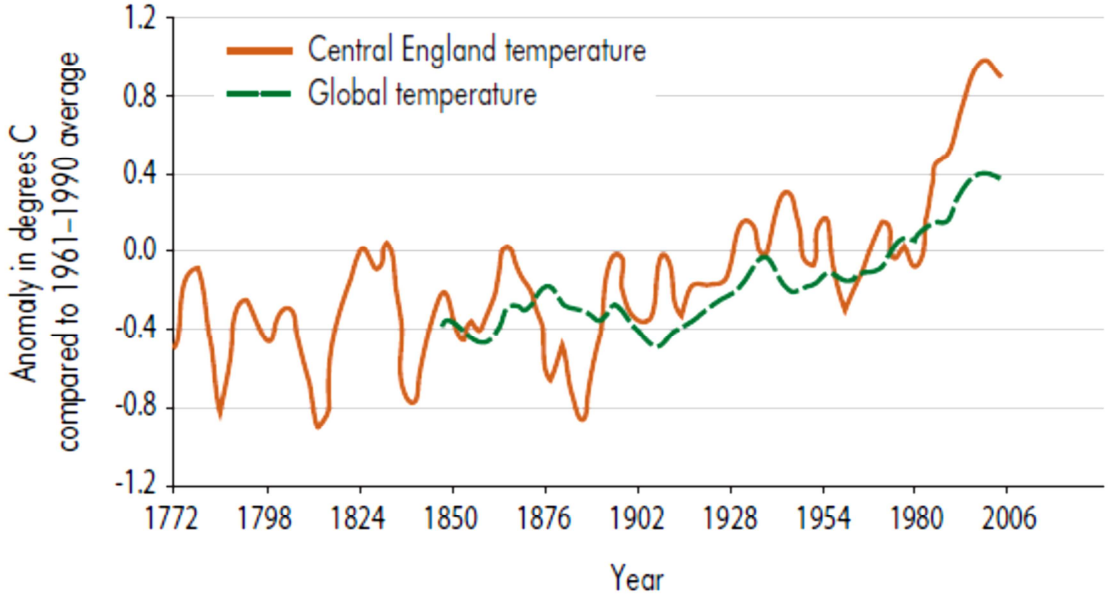


Figure 1.4. Central England surface air temperature (ºC) from 1772 -2008 (source, UKNAE, 2011 (www.uknea.unep-wcmc.org))

With regards to the effects of these drivers on birds, a range of ecological responses have been reported in indicator species. For example, changes in distribution have been associated with increasing temperature, with southern species moving their southern distributional edge an average of 19 km northwards (Thomas & Lennon, 1999). Also changes in phenology (i.e. arrival dates) have been described with earlier arrival dates observed in a number of species due to warmer springs (Sparks, 1999; Crick & Sparks, 1999). Population changes have also been reported in relation to land use change of different habitats (Fuller et al., 2002; Newton, 2004).

In light of these species responses and the already established monitoring schemes, birds have been already used by UK policy-makers as bioindicators.

The wild bird index has been adopted by the UK Government as one of its 15 headline indicators of sustainable development (Gregory et al., 2003) (Fig 1.5).

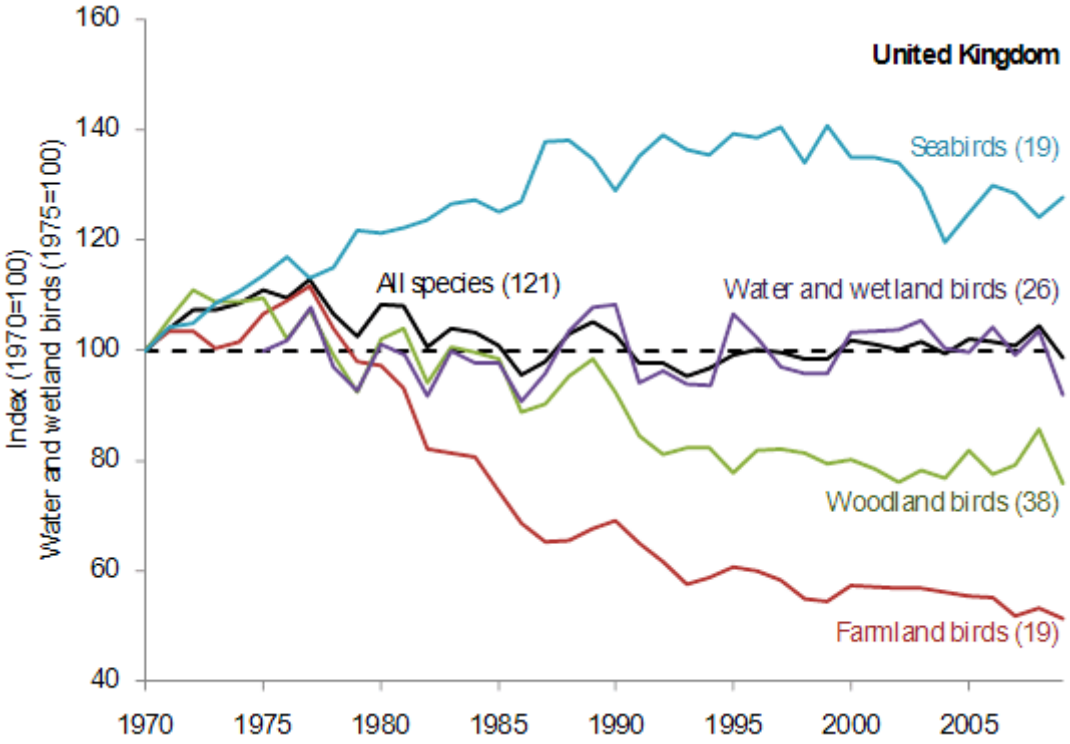


Figure 1.5 UK Biodiversity Indicator: Populations of wild birds (1970-2009) (source, Bioindicators, www.bto.org)).

This indicator is a composite of population trends of species grouped by geographic region or ecological associations, namely their specialisation on particular habitats for breeding and it aims to measure population trends of a large suite of birds to act as a barometer of ecosystem health (Gregory et al. 2005; Gregory & van Strien, 2010). In addition, this index also intends to promote and encourage the development of other national bird population monitoring schemes that can help collect further data on the status of the environment (Gregory & van Strien, 2010). In the case of the UK, this index has shown that common birds in both farmland and woodland are in sharp decline so DEFRA has pledged to reverse this decline for farmland birds by 2020 using this headline indicator to measure their progress (Gregory et al., 2003). However, primary biological traits of birds are not currently used to delineate indicators.

National governments and the EU are increasingly using this type of tool to assess sustainable development strategies, environmental and ecosystem health (Gregory & van Strien, 2010). Hence, it is essential to be able to investigate and understand how direct and indirect drivers work together and how these, in turn, affect ecological systems. Once we have this information, the importance of the conservation of biodiversity and ecosystems can be highlighted to governments, private sector and general public and adequate conservation measures implemented (Watson, 2005).

In order to be able to link multiple, interacting drivers of change to the response of ecosystems (i.e. bioindicators) and their services, predictive models are needed (Lee & Jetz, 2008; La Sorte & Jetz, 2010; Cardillo et al., 2012). Such models will not only help us to better understand how ecosystems respond to changes in the drivers, but they will also allow us to quantify the differential costs and trade-offs of various policies and interventions, which is the type of information that is needed to influence policymakers to make informed decisions, that are beneficial to biodiversity and ecosystem functioning (Watson, 2005).

1.4 Ecological models as tools for linking ecological responses to environmental pressures and evaluating optimal design of indicators. Scope of this thesis.

For centuries humans have observed and recorded the relationships between species and their environment. Whilst the earliest records were mainly qualitative notes (Grinnell, 1904) nowadays numerical models are used for both describing patterns and making predictions in space and time (Elith & Leathwick, 2009). These early studies described biological patterns in terms of their relationships with geographical and/or environmental gradients (Grinnell, 1904) but as these studies evolved and linked individualistic responses of species to their environment they provided the base for modelling individual species responses in a variety of ways (Elith & Leathwick, 2009).

Clearly, it is important for the conservation of biodiversity to understand the relationship between external drivers of environmental change, intrinsic species characteristics and the synergy among all these factors. This project, therefore, aimed to identify (a) those characteristics make species more vulnerable to environmental change and (b) those environmental pressures to which species are most sensitive. These were assessed with respect to the passerine avian group in the UK as a case study.

Since birds are relatively easy to detect and identify, they are a particularly useful group for the study of environmental change (Gregory et al 2004). For example, a total of 215 bird species breed in the UK on a regular basis (Gibbons et al 1993) and over 80% of those species are censed or surveyed on an annual basis through a variety of surveys supported by government and non-government conservation organisations (Gregory et al 2004). In particular, passerines make an ideal test case to investigate the relationship between ecological responses to environmental change and particular life history characteristics because of the ecological and behavioural diversity shown by members of this taxon. Besides, there are extensive surveys based on point counts for this taxon worldwide which are considered to be particularly suitable for monitoring populations (Seoane Carrascal, 2008).

In terms of the analytical methods that could be used to investigate the different impacts of environmental change on species, there is a range of techniques that can be used to study this processes. Quantitative modelling and mapping of species distributions developed as a consequence of the combination of: i) field-based studies looking at habitat and species associations and, ii) linear multiple regression and discriminant analysis (Schauffer, 2002). These studies allowed for a deeper understanding of the relationship between species locations and concurrent environmental patterns through statistical methods that provided coherent treatments for error distributions of both presence-absence data and abundance (Elith & Leathwick, 2009).

General linear models (GLMs) followed these enabling for a more sophisticated and realistic approach thanks to features such as non-normal error distributions, additive terms or non-linear fitted functions (Elith & Leathwick, 2009). These models have been used to look into population trends in a variety of taxa and their relation to different environmental pressures and species characteristics to try to determine what could be the possible causes of the observed trends (e.g. amphibians, McGrath & Lorenzen, 2010). As mentioned before, particular traits may confer on species the ability to adapt to particular environmental changes. Therefore studies examining the association between species ecological responses and characteristic traits would be of significant value to identifying particular species' syndromes or traits that could be target for conservation programmes or be used as part of monitored schemes as part of bioindicators .Though this methodology has already been used in a variety of studies looking into the matter (Brädle et al., 2002; Jiguet et al., 2007; Reif et al., 2008; Van Turnhout et al., 2010), no single study has yet tried to combined a range of species traits (including life history, resource use and phenological). Therefore this thesis used a combination of linear and regression models to understand the relationship between observed population trends, species characteristics and phylogenetic relationships. [Chapter 2]

Rapid advances in physical geography have also provided new data and new methods that allowed robust and detailed information about both marine and terrestrial environments (Elith & Leathwick, 2009). Species distribution models (SDMs) have been undergoing phenomenal development in the past decades as estimates of environmental conditions across entire landscapes are now readily available thanks to Geographical Information Systems (GIS). SDMs have allowed for a more in depth and detailed study of the relationship between environmental predictors and presence or abundance of species by providing detailed predictions on these interactions (Elith et al., 2006). As such, they have allowed scientists to: i) investigate species responses to different environmental gradients and environmental pressures, ii) investigate the characteristics of the

environment that allow species to persist, and iii) predict species distribution in both the past and the future (Elith et al., 2006).

Another traditional way of looking at species distributions and their responses to environmental pressure has been through the use of species extinction and colonisation probabilities. The estimation of rates of change in biodiversity and the factors driving it are fundamental for establishing conservation actions. In fact estimates of species' extinction risk (i.e. IUCN Red List Indices) are already used in different programmes to measure progress towards different conservation targets (Butchart et al., 2005). These colonisation extinction models entail a more dynamic approach to species distribution analysis since data for at least two different time periods is required to calculate the extinction and colonisation rates. They also allow for a more dynamic study of the relationship between species and the environmental pressures where responses and changes in drivers can be analysed simultaneously. New approaches that combine traditional general linear models with more advanced Bayesian statistics have recently been developed (Raftery et al., 2010) allowing for a more robust model selection methodology thanks to the inclusion of a measurement of parameter uncertainty (Wintle et al., 2003).These models have been used to study a variety of aspects of animal and plant ecology (e.g. mussel growth rate, Jiao et al., 2008; algal bloom prediction, Hamilton et al., 2009), but this thesis represents the first attempt to apply this methodology to the study of environmental drivers of colonisation and extinction rates on a bird assemblage. [Chapter 6]

Recently it has been recognized that some key elements of species ecology have been largely missed from species distribution models: i) the lack of reference and inclusion of biotic interactions (Araujo & Luoto, 2007), ii) the distinction between geographic and environmental spatial structure.

In terms of species interactions (e.g. species competition or predation) it has been suggested that they may play a small but significant role in governing

species distributions (Pearson & Dawson, 2003). Although from a theoretical point of view single species models will be favoured to understand their particular behaviour to environmental drivers and pressures, it is well-recognized that species distribution models and response curves are an expression of their realized niche (Hutchinson, 1957) and are influenced by the presence of other species (Austin et al., 1994). In order to deal with this issue, other approaches have been proposed.

On one hand, community methods have been seen as a potential answer because they carry additional information present in the wider community that may help to better informed the modelling of the relationships under study (Elith et al., 2006). In fact it is understood that important but subtle environmental trends may only be apparent in the response of multiple species where relevant predictors have been retained because of the strong community signal that otherwise may be lost in single species models (Elith et al 2006). The efficiency of community models in representing species-environment relationships in comparison to single species models has already been tested in, for example, vegetation communities with community models being more efficient at simulating landscape patterns (Zimmermann & Kiennast, 1999). Also these type of models have been recently been applied in studies looking at the difference in relative importance of different environmental pressures driving species distributions which would be of critical importance when determining and assessing impacts of pressures on species and ecosystems (e.g. Titeux et al., 2004; Beisner et al., 2006; Kivinen et al., 2007; Hajek et al., 2011) These community multivariate techniques abet the study of species within a community setting in relation to their response to environmental gradients and have been successfully used in vegetation and animal studies for decades (Mitchell, et al., 1998; Choler et al., 2001; Meyer et al., 2008). In this project these techniques have been used to not only look at the passerine group in the UK in relation to other bird assemblages but to also examine the change in importance of environmental drivers between time periods which probably

represents one of the first attempts at this type of temporal analysis in this animal group. [Chapter 3 and 4].

Niche concepts and models have too been suggested as possible alternatives of investigating species responses to changes in the environment. By looking at species distribution in the environmental space (i.e. niche) described by a particular set of predictors (e.g. climate, land use or both), researchers have tried to determine species potential or vulnerability in terms of environmental change (Thuiller et al., 2005). This is done by quantifying particular niche parameters such as tolerance or niche breadth and relating those to potential/expected changes in the described environmental space (i.e. climate change or land use change). This approach not only allows for the potential inclusion of a variety of predictors to describe the species' environmental space but can also provide a variety of parameters that could be used to monitor and quantify species responses to environmental change. In this study we used traditional and novel approaches of describing species niche parameters and investigate the importance and impact of environmental variables in driving species responses. This not only represents one of the first efforts to describe environmental niche characteristics for these group but also a different approach when looking at the impacts and species responses to environmental change. [Chapter 5]

With regards to geographical and environmental spatial patterns, with the inclusion of more sophisticated spatial data, the issue of spatial autocorrelation arose when developing species distribution models (Elith & Leithwick, 2009). Spatial autocorrelation occurs when the values of predictors sampled at nearby locations are not independent from each other, which can be due to: i) biological processes such as dispersal, speciation, etc.,ii) non-linear relationships between environment and species, iii) models' failure to account for an important environmental variable that is spatially structured (Legendre & Legendre, 1998). In most cases spatial autocorrelation is seen as posing a serious problem when testing a model as it violates the assumption of random

error distribution (Dorman et al. 2007). A number of methods have been developed to deal with this issue (Dorman et al., 2007) for example : i) Moran's I plots were developed to establish the presence of spatial correlation in the data (Legendre & Legendre, 1998), ii) autocovariate models address the issue by extending a GLM through the addition of a distance-weighted function of neighbouring response values to the model's explanatory values, iii) spatial eigenvector mapping, which are based on the idea that the spatial arrangement of points can be translated on a series of explanatory variables which capture the spatial effects at different spatial scales, iv) spatial generalised linear mixed models (GLMMs) where the random effects and within-group errors may be spatially autocorrelated. These methods allow studies to deal with spatial autocorrelation and allowed model predictions to be more reliable and accurate with regards to their estimates of species- environment relationships and the importance of particular environmental predictors. Throughout this thesis methods have been implemented to assess spatial autocorrelation of data and quantify their effect on the analysis to enable for more robust model results. This represents an improvement on the most common and general used methods in the field [Chapters 3, 4, 5 and 6]

Furthermore, species are known to respond to their environment at specific scales and may show different responses to environmental predictors according to the scale considered (Bellier et al., 2007). Therefore the above mentioned approaches would also help identifying at which scales different processes are operating which would be key in further the understanding between environmental predictor/ pressure and species distributions (Wagner and Fortin, 2005; Bellier et al., 2007).

One final development that has recently become more relevant in species distribution models has been the inclusion of phylogenetic data to investigate if the drivers and the consequences of biodiversity loss are somehow related to species evolutionary history (Lavergne et al., 2013). Traditionally phylogenies were used to study the evolution of ecological traits and relationships among

species in communities but they can also be used to understand the global patterns of biodiversity (by studying biogeographical patterns within and among clades) and to understand current functional groups patterns within communities by for example looking at the potential relationship between phylogenetic relationships between species, their characteristics traits and how this might influence of species environmental adaptability (Wiens & Donohhue, 2004). Even though not all current methods allow for inclusion on phylogenetic information in models, when possible this data has been taken into account in the analysis to include the effects of phylogeny and improve the robustness and accuracy of the models. [Chapters 2 and 6]

The results from the above outlined analysis were expected to aid identification of potential new ways of improving current bio-indicator indices for development of future conservation policy and legislation to halt loss of biodiversity at national and regional scales. The following specific questions were tackled:

- Are passerine species with particular ecological or life history characteristics more vulnerable to population declines? [Chapter 2]
- What is the relative importance of climate, land use, pollution and biological factors as drivers of current avian assemblage patterns in the UK? [Chapter 3]
- What are the major changes observed in the relative importance of key environmental driver over time on the UK passerine community? [Chapter 4]
- How do species characteristics relate to community model accuracy? [Chapter 4]
- What are the main external factors driving changes in species' niche characteristics? [Chapter 5]
- Which species traits are associated with ability to track environmental changes? [Chapter 5]
- How do niche characteristics relate to species current conservation status? [Chapter 5]

- What are the key environmental drivers and species characteristics operating colonisation and extinction dynamics in the UK? [Chapter 6]
- Are there any particular interactions between traits and drivers that produce particular colonisation or extinction patterns in species? [Chapter 6]

Using the set of environmental drivers outlined in Table 1.1.

Table 1.1. Environmental drivers use in the different thesis chapters

Environmental driver	*Chapter*
Climate (i.e. temperature, precipitation)	3, 4, 5, 6
Land use (i.e. area of different land uses)	3, 4, 6
Pollution (i.e. concentration of key pollutants)	3, 4,5
Land use intensity (i.e. livestock density, human population),	3, 4 6
Competition (i.e. number of potential competitors),	
Predation (i.e. number of potential predators).	
Space (i.e. measure of data spatial patterns)	3, 4, 5, 6

Chapter 2 : Long term population trends in UK passerines: are there specific traits or syndromes conferring population resilience?

This study has been published as a scientific article:

Salido, L., Purse, B.V., Marrs, R., Chamberlain, D.E., Shultz, S.. 2012 Flexibility in phenology and habitat use act as buffers to long-term population declines in UK passerines. *Ecography*, 35 (7): 604-613.

Abstract

Ecological responses to environmental change are wide-ranging, from alterations in the timing of life-history events to range and population changes. Explaining the variation across species in these responses is essential for identifying vulnerable species and for developing adequate conservation or mitigation strategies. Using population trend data from the UK Breeding Bird Survey, this study examined the association between long-term population trends (1994-2007) and phenological, life-history and resource-use traits of UK passerine species. Phenology, as well as productivity and resource use were significantly associated with long-term population trends. Average laying date and first clutch laying period were key predictors, with higher population growth rates associated with earlier laying dates and longer laying periods. This suggests that flexibility in the duration of reproductive periods buffers species against environmental changes. Average laying period was particularly important for migrant species. Flexibility in laying dates for these species is constrained by their arrival dates; mean change in arrival date over a twenty-five year period strongly predicted population trends amongst migrant species. Besides the key role phenological flexibility plays in buffering population declines, we also showed that more productive, generalist species were less likely to have declining populations than species with specialized habitat requirements, particularly those associated with farmland and urban areas and those reliant on highly seasonal food items (i.e. invertebrate eaters). These results underscore the need for a multi-faceted approach to understanding the mechanisms governing population trends. Additionally, species' sensitivity to

environmental change is likely to depend on interactions between species-specific phenology, habitat and resource-use traits.

2.1 INTRODUCTION

There is compelling evidence that human activities are leading to climate change, resulting in increasing pressure on terrestrial biodiversity (Jetz et al. 2007; Rosenzweig et al. 2007). Ecological responses to recent climate change are wide-ranging, including alterations in the timing of life-history events (arrival of migrants, appearance of butterflies and flowering, Both & Visser, 2001; Crick, 2004; Parmesan, 2006), range changes (Parmesan et al. 1999; Thomas & Lennon, 1999; Parmesan, 2007) biodiversity loss (Lemoine & Böhning-Gaese, 2003) and population dynamics (Julliard et al., 2004; Both et al., 2006). Climate change, however, is not the only environmental change affecting biodiversity. Habitat loss and modification are also known to be key drivers of population change. For example, the widespread population declines and range contractions in farmland birds in the UK in the last 50 years have been linked to agricultural intensification (Chamberlain et al., 2000; Vickery et al., 2001; Benton et al., 2002; Newton, 2004; Atkinson et al., 2005).Various other studies in Europe have reported significant declines in populations of both woodland and farmland specialist birds which could be partly attributed to increasing intensive management practices of both forests and farmland (Julliard et al., 2003; Gregory et al., 2007).

As there is substantial inter-specific variation observed in the magnitude and direction of responses to environmental change, identifying the mechanisms underlying species' responses is essential for developing adequate conservation strategies for the most vulnerable species (Jiguet et al., 2009; Végvári et al., 2009). Across Europe, threats to wild birds and to other elements of biodiversity are currently monitored using population changes in indicator species from different breeding habitats (Newson et al. 2004; Gregory et al.

2005). Woodland and farmland breeders are thought to be at greatest risk from habitat fragmentation (Chamberlain et al., 2000; Atkinson et al. 2005; Amar et al., 2006; Hewson & Noble, 2009) and the latter are targeted in the UK by management options such as use of wild bird seed mixture and skylark plots under Environmental Stewardship schemes (Vickery et al. 2004). A greater understanding of the mechanisms underpinning species' differential responses to environmental change may be obtained by relating responses to biological traits. For instance, life-history and resource use traits have been associated with avian population trends. Productivity and brood number have been found to have positive effects on population trends (Végvári et al., 2009) whereas larger body sizes and longer development periods have been linked to with decreasing populations. On the other hand, diet richness, diet type and foraging and nesting habitats can all be considered as proxies for resource flexibility. The more resources a species exploits (i.e. food items, habitat types, etc), the better it should be able to adapt to changing conditions (Sandvik & Erikstad, 2008).

Despite the increasing evidence of phenological responses to climate change in a range of bird species, few studies have looked at the relationship between observed population trends and phenological traits. The annual cycle of birds is made up of different phases that appeared to have evolved so that the different events (i.e. moult, migration, breeding) take place at the most appropriate time of the year (Stenseth & Mysterud, 2002; Bradshaw & Holzapfel, 2006; Dawson, 2008; Carey, 2009). For many species, the period in which young are provisioned is the most expensive stage of the annual cycle; therefore, optimizing the timing of breeding has a significant impact on the reproductive success and fitness of individuals (Carey, 2009). If changes in environmental conditions (due either to climate change or habitat transformation) alter the optimal timing for breeding, species' adaptation potential will depend on their ability to alter their phenology. For example, Coppack & Both (2003) suggested that the phenology of breeding events is likely to be key to a species' ability to adapt to changing conditions in seasonal environments. Strong selection

pressure for matching offspring needs with peak food abundance and minimizing the cost of reproduction at the egg-laying stage can result in flexibility and differential responses amongst a range of species traits (Visser, 2008; Carey, 2009; Moussus et al., 2010). In fact, advanced onset of breeding and extended reproductive periods are putative responses of birds to climate change with 60 per cent of species studied in the UK presenting advances in laying date (Crick et al*.,* 1997; Crick & Sparks, 1999).

Of those few studies considering relationships between population trends and phenological traits, Møller et al. (2008) observed that bird species that had not advanced their spring migration dates were more likely to have declining populations than those that had. Van Turnhout et al. (2010) also found that, in the Netherlands, ground-nesting, late-arriving migrants had suffered the largest population declines. Hence, exploring trade-offs between phenology or phenological flexibility and other ecological characteristics may provide insight into mechanisms underlying the links between phenology and population trends. For example, it has been reported that phenological changes are sensitive to both the number of broods and clutch size, with single brooded species shifting their laying dates more than multiple brooded ones (Visser et al., 2003). However, the degree of flexibility in these traits additionally may be constrained by other characteristics such as migration. Moussus et al. (2010) showed that the degree of flexibility in phenology was associated not only with climatic and ecological niche breath but also with migration. Long distance migrants and specialist species being less adaptable than resident and generalists species. Migratory behaviour has also been linked to bird responses to changes in climatic conditions (Lemoine & Böhning-Gaese, 2003; ; Gordo & Sanz, 2006; Rubolini et al*.,* 2007; Møller et al., 2008) with residents and short-distance migrants appearing more responsive to climate change than long distance migrants (Lehikonen et al., 2004; Rubolini et al., 2007; Thorup et al., 2007). Resident species are exposed to cues year-round that allow them to match their phenology to local environmental changes, whereas long-distance

migrants will experience changes in their breeding ranges only after they return from their over-wintering grounds (Végvári et al., 2009).

In order to identify which species traits are most strongly associated with long-term trends, impacts of phenology, life-history and resource use must be evaluated within the same model framework. This study aimed to identify the key species-specific traits and trait interactions associated with population trends for 50 passerine species in the UK over a 13 year period (1994-2007) using a comprehensive species database that includes key phenological traits (i.e. average laying period) that may help us understand further the mechanisms by which species adapt to phenological changes in their environment. Passerines were chosen as the case study because of the ecological and behavioural diversity shown by members of this group. Moreover, 50% of the species we focus on are used in the calculation of the UK woodland and farmland bird indices.

The main aims were to: evaluate the relative contribution of phenology, life-history, and resource use as predictors of population trends in passerines and a subset containing migrant species; to identify whether particular types of phenological flexibility (i.e. change in arrival date, average laying periods) render species less vulnerable to declines; and assess the relationship between migration and phenological flexibility.

It was predicted that species with the following traits will be prone to population declines: large body size, long development periods, migrants and farmland and woodland breeders. Conversely, more productive species, and diet and habitat generalists will be more likely to have increasing populations. In addition, those species with phenological flexibility, such as those that lay early, have long breeding periods and are resident or partial migrants will be better able track and respond to changes in optimal breeding periods resulting from climate changes. Furthermore it was expected the effects of phenological flexibility to be even more crucial for migratory species; migratory species able to advance

arrival dates, lay earlier and breeding for longer periods should be less likely to show declining trends.

2.2 METHODS

2.2.1. Species data

Data on the population trends of passerine bird species in the UK were extracted from the BTO/JNCC/RSPB Breeding Bird Survey (BBS). The BBS was introduced in the UK in 1994 to provide precise information on the year-to-year and longer-term change in population levels across a broad spectrum of common species across a range of regions and habitats (Gregory et al., 2004). The BBS is a survey-based monitoring programme where 1km squares are selected randomly within regions stratified according to human population size and surveyed using a line-transect methodology (Risely et al., 2008). Population changes are estimated using log-linear models with Poisson error terms. Counts are modelled as a function of year and site effects, weighted to account for differences in sampling effort across the UK, with standard errors adjusted for over-dispersion (Risely et al., 2008). For this study the instantaneous growth rates were used as the measure of the long-term population trends (see Appendix). These were calculated as the slope of the overall Poisson model output indices for each of the 50 passerine species over the 13 years of available data (1994-2007). The standard errors around these slopes provide a measure of the reliability of the estimated growth rates. Some breeding passerine species were excluded from the study due to a lack of data on their growth rates or phenological traits (e.g. sand martin, house martin, rook).

2.2.2. Explanatory variables

Within each suite of biological characteristics, potential traits and interactions, which might explain population trends, were selected *a priori* on the basis of evidence from previous studies (Brändle et al., 2002; Jiguet et al., 2007; Reif et

al., 2008; Végvári et al., 2009). Resource use and life-history variables were mainly extracted from Snow and Perrins (1998) and relevant ecological studies carried out in the UK (i.e. Siriwardena et al., 1998; Newson et al., 2004; Gregory et al., 2007). The fifteen trait variables selected as candidate predictors are summarised below and in Table 1.

Phenological traits. Data for laying dates and first clutch laying periods were obtained from the Nest Record Scheme (NRS, Crick et al., 2003). This scheme started in 1939 and it currently collects c. 30,000 individual nest histories per annum for *c.*120 bird species from the UK; this represents one of the longest and largest scale datasets on breeding phenology in Europe. Initial analysis of the NRS data for 65 bird species (including passerines) over a 25 year period (1971-1995) showed that 20 of those species exhibited statistically significant trends towards earlier laying and only one had become significantly later (Crick, 2004). Laying dates represent the average Julian date on which the first clutch may have been laid excluding extremes and for species where precision was within 5 days (64-167 Julian date). First clutch laying period represented the number of days between the earliest and latest recorded date (23-106 days)(for further details on the quality of nest record scheme data and estimation of laying dates please refer to Robinson, 2005). *Migratory behaviour* was obtained from Dudley et al. (2006), and divided into three categories representing resident, partial migrants and migrant species. For the migrant analysis, mean change in arrival dates (0.4-0.01 days) was extracted from Sparks et al. (2007) while migration distance (19.6- 68.1 ˚ latitude) was acquired from Møller et al. (2008).

Resource use. Habitat was classified into 6 different categories (i.e. generalist species, farmland species, woodland species, wetland species, urban species and upland species) according to the main habitat preferences reported for the species in the UK (Newson et al, 2004). This type of classification has not only been used in previous studies (Jiguet et al., 2007, 2009) but also represents the main habitats for which specific bird indicators have been developed nationally

and regionally (Newson et al., 2004; Gregory et al., 2005). Data on food items for each species was extracted from Snow and Perrins (1998). Two aspects of diet were quantified; species were assigned to a diet group according to whether their main diet items were of plant, insect or mixed origin. with seven diet groups (i.e. small seed diet, large seed diet, insect diet, invertebrate diet, generalist, generalist with carrion, highly specialist) identified through hierarchical clustering analysis using the package *pvclust* in R (for more details on data analysis see supplementary data). Also diet richness was compiled using the total number of items extracted from Snow and Perrins (1998) for each species (24- 219 items).

Life-history traits. The number of broods per season, productivity, average body weight, nesting periods and clutch size serve as key life history traits and are likely to be related to a species intrinsic growth rate. Average body weight was calculated as the mean of the male and female value for adult body weight (range across species: 5.75- 1189gr). Productivity (3.5-19.5 eggs/year) was calculated as the product of the average clutch size (3.5-10.5 eggs) for the species and the average number of broods in a year (1-3 broods/year). Incubation and fledging periods were summed to represent average nesting period which refers to the average number of days of incubation and fledging reported for each species across years(24- 61.5 days).

2.2.3. Analysis of relationships between species-specific traits and population trends

The association between species traits and population trends was examined using Linear Models implemented in the R software package (R development Core Team, 2008).

In order to reduce the number of factors evaluated in the model selection procedure and to minimize the risk of multi-collinearity among predictors, GVIF (generalized variation inflation factor) and Pearson correlation coefficients were used to determine which variables were highly correlated within each suite of

traits. Variables were considered collinear when GVIF > 5 or r^2 > 0.7. Furthermore, each predictor trait was tested using univariate linear models to determine their individual effect on population change (see Appendix B) and in case of variable collinearity only the variable with higher explanatory power in univariate analysis was selected for the predictor pool for the multivariate modelling (see further details below) (Appendix A).

Then the relative importance of predictors was evaluated using *relaimpo* analysis implemented in the R software package with the same name. Relative importance can be defined as "the proportional contribution each predictor makes to R^2, considering both its direct effect (i.e. its correlation with the main response variable) and its effect when combined with the other variables in the regression equation" (Johnson & Lebreton, 2004). The metric *lmg* was used. This partitions R^2 by averaging over orders following Lindeman et al. (1980). The *lmg* has been recommended as the most adequate metric to calculate relative importance of predictors because it not only represents the mean contribution of variables over bootstraps runs in models of different sizes but also uses both direct effects and adjusted effects for other variables in the model (Johnson & Lebreton, 2004; Grömping, 2006;). The *lmg* also allows for the inclusion of interactions and model weights. Key interaction terms (between pairs of variables including at least one categorical variable) were selected for inclusion in the global model on the basis of exploratory coplots, provided trait groups contained adequate, balanced sample sizes.

The final model was determined using weighted general linear models (GLM) with a stepwise optimal model selection procedure based on corrected AIC (AICc) values. The response variable, the estimate of annual growth rate, was weighted by the inverse of its standard error as a measure of reliability. This process provided a correction of trend estimates by allowing a greater contribution to the model of species with more reliable growth rate estimates (Jiguet et al., 2009). In order to identify the impact that weighting had on the final model, unweighted models were also calculated (see Appendix).

Table 2.1. Description of species-specific traits used in the long term population trend analysis. Species-specific values of population growth rates and main trait predictors used for the final model can be found in Appendix A.

Trait group	*Variable*	*Description*	*Data source*
Phenology	Average laying date	Median date of the 1st egg laying (Julian day)	Robinson (2005)
	Average first clutch laying period	Latest recorded date- earliest recorded date (no. days)	Robinson (2005)
	Migration strategy	Nominal variable: Resident species (1), partial migrant species (2) and migrant species (3)	Dudley *et al.*(2006)
	Mean change in arrival date (only for migrants)	Mean change in observed date of arrival (no.days)	Sparks *et al.*(2007)
	Migrating distance (only for migrants)	Mean in ˚ latitude between wintering and breeding grounds	Møller *et al.*(2008)
Resource use	Diet type	Nominal variable: small seeds eaters (1), large seed eaters (2), insect eaters (3), invertebrate eaters(4), generalist (5), generalist+carrion (6), highly specialist (7)	Snow and Perrins (1998)
	Diet richness	Number of items per category in the diet of each species	Snow & Perrins (1998)
	Nest location	Nominal variable: Ground (0), vegetation (1), hole (2)	Snow & Perrins (1998), Siriwardena *et al.*(1998)
	Habitat preference	Nominal variable: Generalist (1), farmland specialist (2), woodland specialist (2), wetland specialist (3), urban specialist (4), Upland specialist (5).	Newson et al. (2004)
Life history	Average body weight	Average body weight for the species (♀♂)(g)	Snow & Perrins (1998)
	Productivity	(Average clutch size) x(Average brood size/year)	Snow & Perrins (1998)
	Average clutch size	Average number of eggs per clutch	Snow & Perrins (1998)
	Number of broods per year	Average number of clutches per year	Snow & Perrins (1998)
	Average nesting period	Average number of days spend in the nest including incubation and fledging (no. days)	Robinson (2005)

To verify the robustness of the final model, a bootstrap procedure was implemented using the R package *boot.StepAIC* (Austin & Tu, 2004). In this method, 999 random bootstrap samples were drawn repeatedly from the original dataset to investigate the variability of model selection under the AIC stepwise algorithm (Austin & Tu, 2004). Within each bootstrap sample, backward and forward selection was used to determine the most parsimonious predictive model (for further details see Austin & Tu, 2004). This technique determines a variable's likelihood of being identified as an independent predictor (Austin & Tu, 2004). Models were also constructed for all variables in the predictor pool (global model) and without any variables (null model) to assess the value of the final model. Shapiro tests and diagnostic plots were used to evaluate the normality of model residuals and to identify outliers. If outliers were identified, models were refitted without those species to evaluate the robustness of trait relationships.

Finally, to evaluate the impact of phylogenetic non-independence between species on model selection and performance, phylogenetic generalized least-square (PGLS) regression (Freckleton et al., 2002) was used, implemented in R using the *caic* package (Paradis et al., 2004). The expected covariance between species was calculated on the basis of the phylogeny developed by Thomas (2008). Lambda, or the weighting of species covariance matrix, was optimised using a maximum likelihood approach (Pagel 1999). Values of lambda vary between 0 and 1, with 0 indicating no phylogenetic autocorrelation or phylogenetic autocorrelation proportional to branch length respectively. Branch lengths were available and were standardised across the species-covariance matrix. We used the same predictor variables selected during the GLM procedure, assuming a Brownian model of trait evolution, (Butler & King, 2004) (see Appendix for further details).

Selection between PGLS regression models and GLMs was made on the basis of AIC_c and adjusted D^2 (Nagelkerke, 1991). This allowed for comparison between models (non-phylogenetic and phylogenetic) with different numbers of

parameters and therefore selection of the minimum adequate model amongst all possible alternatives.

Mean values of key predictors in final models were compared between trait groups using Student's t-tests where group variances were equal and Welch t-test (Welch, 1947) otherwise.

2.2.4. Migrant passerine species in the UK

Since migrant species have been shown to be particularly affected by changes in environmental conditions we ran a specific model for these species that included both variables selected by the best overall species model and some other phenological traits thought to influence their ability to respond to environmental change, namely migration distance (Møller et al., 2008) and mean change in arrival date (Sparks et al., 2007). Information on migration distance and mean change in arrival date was available for 14 of the 15 migrant species included in the overall passerine analysis, hence only these species were used for the analysis. The final model was selected using the same procedure as indicated above for overall species.

2.3. RESULTS

2.3.1. Relationships between passerine traits

Average brood size and average nesting period were excluded from the initial predictor pool based on their high GVIF and *r* values (GVIF=95.2, *r*= 0.7 and GVIF=14.7, *r* =0.7 respectively). Average clutch size was also dropped due to its high GVIF (32.0).

2.3.2. Traits governing population trends of UK passerines

Life-history, phenological and resource use traits were all represented amongst the predictors that best explained variation in observed growth rates (Table 1.2a). Amongst these, habitat and migration strategy were the most important factors explaining variance in the observed growth rates causing the largest change in AIC_c when dropped from the model (Table 2.2b). Coefficient values for selected predictors indicated that species that were resident, more productive, with earlier laying dates, used wetlands as their main habitat and had a diet mainly based on large seed or general diets were more stable or had increasing population trends (Table 2.2b). The interaction between first clutch laying period and migration behaviour was highly significant indicating that migrants with longer first clutch laying periods had significantly larger positive growth rates (r^2=0.33, $F_{1,13}$=6.31, p = 0.002, Fig 2.1c). No such trend was observed in resident species (Fig 2.1a). For partial migrants there was a weak positive relationship between growth rate and laying period (Fig 2.1b) that became insignificant when the outlier, the stonechat (*Saxicola torquatus*) was removed (see Appendix).

Phylogenetic models did not perform better than non-phylogenetic ones (Table 1.2a, and appendix A). The weighted GLM performed much better than all alternative models (ΔAIC_c<40, Table 2.2a). The value of lambda in the phylogenetic models was close to zero (λ<0.0001), suggesting that phylogenetic autocorrelation does not drive variation in population trends between species (Table 2.2b). Both the null (with no predictors) and overall model including all variables had a worse fit than the final model, suggesting that the final model was indeed the best fit to explain the observed variation in growth rates observed for UK (Table 2.2a).

Table 2.2. Population trend model for 50 UK passerines based on life-history, phenological and resource use traits: a) Model performance for global, null and final models of population trends based on Adj D^2 and AIC_c . b) Predictor contribution and performance for final model. Δ AIC_c was calculated by removing each predictor from the model and calculating the difference in AIC of this model and the final model. Phylogenetic least squares (PGLS) model. *** 0.001<p<0.01; **0.01< p<0.05; * p~0.05.

a)

Model	Variables included	Adj D^2	AIC_c	Δ AIC_c
Null	-	0	244	27.6
Global	as Final + *Nest location*	0.272	293.6	22
Final	*Average body weight+ Productivity+ Average laying date+ Average first clutch laying period + Migration strategy + Diet type +Habitat preference+ Average first clutch laying period*migration strategy*	0.349	271.6	-
Phylogenetic	as Final	-	332	47.8

b)

Predictor (from final model)	Coefficient (SE)	Δ AIC_c	% times selected in bootstrap models
Average body weight	0.005(0.004)	5.08	56
Productivity	0.48(0.14)***	8.52	93
Average laying date	-0.07(0.03)*	0.58	79
Average laying period	-0.001(0.02)	7.03	93
Migration strategy(partial migrant) ¨	-2.26(2.24)	11.34	95
Migration strategy (migrant) ¨	-7.57(3.56)**		
Habitat preference(Farmland)•	-1.5(1.03)	15.64	92
Habitat preference(Woodland)•	-0.84(1.03)		
Habitat preference(Wetland)•	2.67(1.45)*		
Habitat preference(Urban)•	-1.12(1.05)		
Habitat preference(Upland)•	0.26(1.56)		
Diet type(large seeds) ˇ	2.64(1.06)**	6.85	97
Diet type(insects) ˇ	0.35(1.73)		
Diet type(invertebrates) ˇ	-1.87(1.32)		
Diet type(generalist) ˇ	2.64(1.41)*		
Diet type(generalist + carrion) ˇ	0.17(1.95)		
Diet type(highly specialist) ˇ	-0.65(1.34)		
*Average laying period*Migration strategy(partial migrant)* ¨	0.02(0.03)	3.4	84
*Average laying period*Migration strategy(migrant)* ¨	0.18(0.06)***		

•coefficient value corresponds to value for the stated habitat categories over the base-line of generalist species

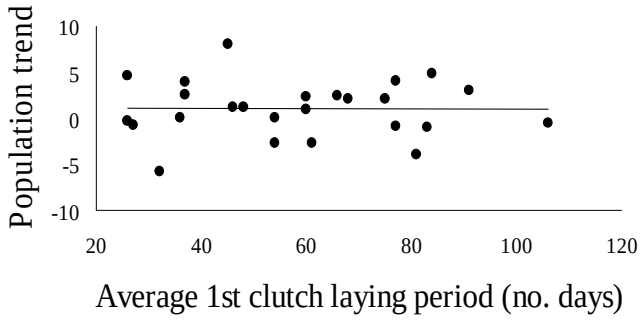
¨coefficient value corresponds to value for migrant species/partial migrants over the base-line of resident species

ˇ coefficient value corresponds to value for the stated diet groups over the base-line of small seed eaters

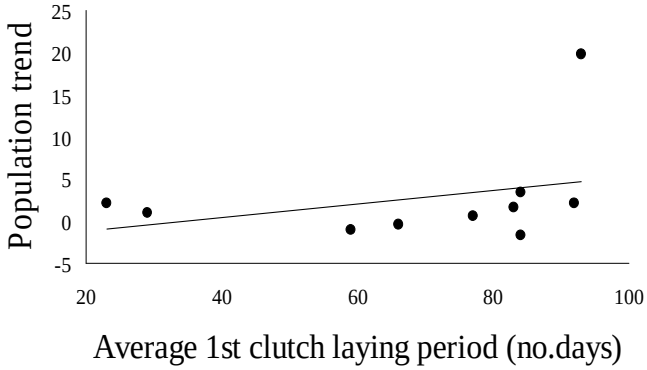
In the overall species model, diet type made the highest contribution to the overall variance explained followed by habitat preference (37% and 20% respectively). The interaction between average laying period and migratory behaviour explained a further 17% while average laying date, productivity and the main effect of migration strategy represented between 9 and 5% of the variance explained. The smaller contributions corresponded to average body weight and the main effect of the 1st clutch laying period (Fig 2.2a).

Although migrant species start laying eggs significantly later than resident and partially migrant species (on average 20 days later), their average laying periods were similar (around 53-69 days) (Table 2.3). Furthermore, resident and partial migrant species had larger productivity than migrant species (by 2 eggs /year). In terms of the habitat groupings, generalists, urban and upland species had earlier laying dates than either farmland or wetland species (~30 days). Woodland and upland species had significantly shorter laying periods than farmland species (by 20 days) but did not differ significantly in productivity (Table 2.3). Generalist species that also included carrion in their diet showed earlier laying dates (by 30-40 days), shorter laying periods (by 20-30) and smaller productivity than the other groups (by 2-5 eggs/year), particularly in comparison to invertebrate and seed eaters (Table 2.3).

a)



b)



c)

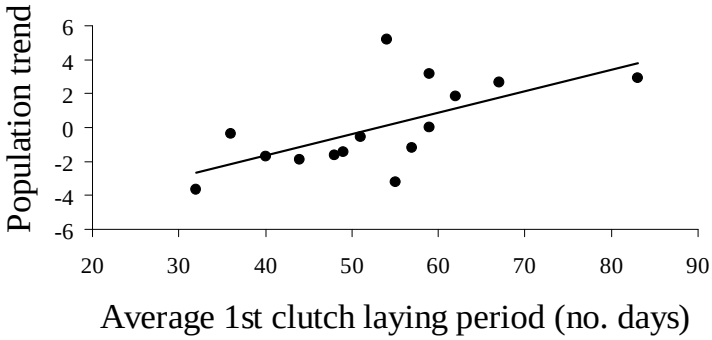
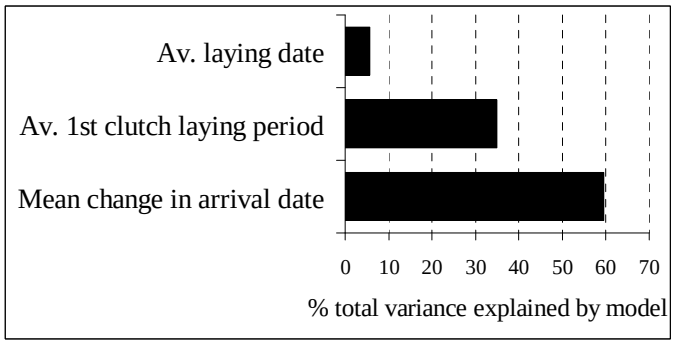


Figure 2.1 The relationship between average 1st clutch laying period and population trend in: a) resident (n=25) , b) partial migrant (n=10) and c) migrant species (n=15). Population trend is expressed as population instantaneous growth rate.

a)



b)

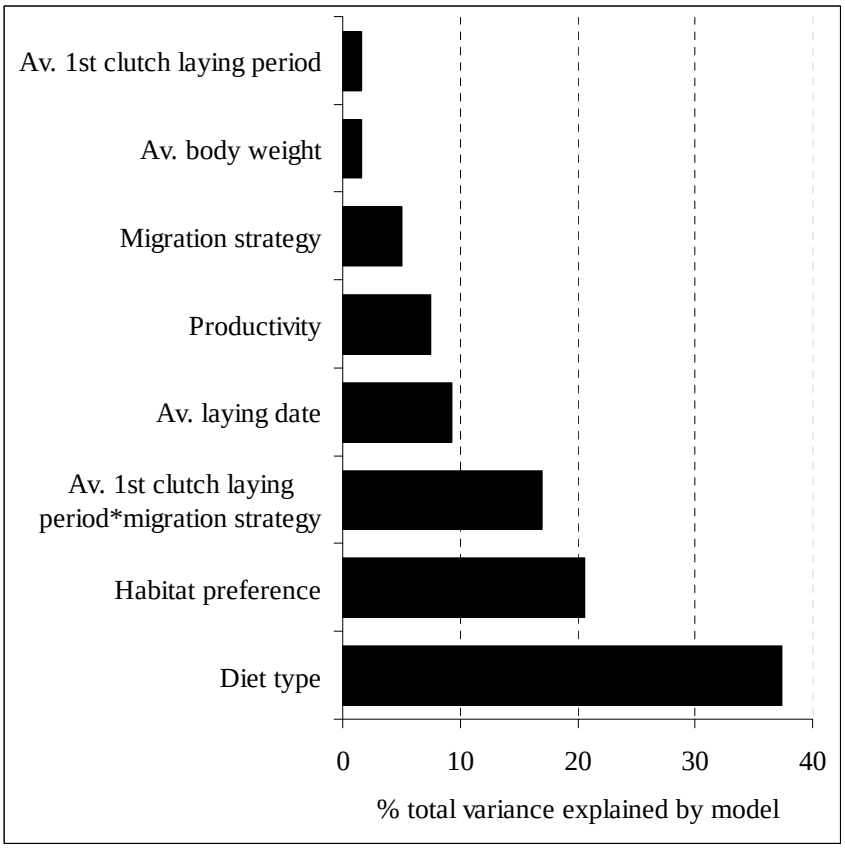


Figure 2.2. Relative importance of species traits. Bars indicate the percentage of the total variance explained (using a weighted model) by each species trait. a) overall species model (total variance explained= 0.655), b) migrant species model (total variance explained=0.865). Av.=Average

Table 2.3. Comparison of mean trait values between different species groups (i.e. migrant strategies, habitat categories and diet groups). *** P ≤ 0.001. ** 0.001 ≤ P ≤ 0.01 * 0.01 ≤ P ≤ 0.1, ^{a,b,ab} represent the groups for which the mean values are significantly different.

Group	Categories	Group means (±SD)		
		Average laying date (Julian date)	Average clutch laying period (no. of days)	Productivity (no. eggs/year)
Migration Strategy	Resident (n=25)	118.2(21.2)^{a**}	58.3(22.3)	9(3.5)^{a*}
	Partial migrant (n=10)	120.1(14.9)^{a**}	69(25)	9.8(1.8)^{a*}
	Migrant (n=15)	140.5(11.1)^{b**}	53.1(12.8)	7(2)^{b*}
Habitat preference	Generalist (n=11)	115.6(16.4)^{a**}	61.6(20)^{ab*}	9.3(2.6)
	Farmland specialist (n=9)	141.9(16.1)^{b**}	74.4(12)^{b*}	9.2(2.8)
	Woodland specialist (n=14)	125.4(16.1)^{ab**}	46.2(12.1)^{a*}	8.4(3.9)
	Wetland specialist (n=4)	143.3(12.7)^{b**}	67.3(7.4)^{ab*}	7.6(2.4)
	Urban (n=8)	115(11.9)^{a**}	62(34.4)^{ab*}	8.6(2.6)
	Upland specialist (n=4)	116.8(36)^{a**}	46(11)^{a*}	6.5(1.9)
Diet type	Small seed eaters (n=7)	133.6(10)^{b***}	78.3(15)^{b**}	9.9(2.2)^{b*}
	Large seed eaters (n=5)	133(9.2)^{b***}	78(17.1)^{b**}	9.3(3.3)^{ab*}
	Insect eaters (n=7)	139(9.1)^{b***}	50.1(9.6)^{ab**}	6.8(1.6)^{ab*}
	Invertebrate eaters (n=8)	130(19)^{b***}	65(16)^{ab**}	10.5(4.3)^{b*}
	Generalist (n=7)	119.1(12)^{b***}	51.7(26.5)^{ab**}	8.3(2.2)^{ab*}
	Generalist+carrion (n=5)	90.4(17.4)^{a***}	42.8(12.5)^{a**}	5.2(1.2)^{a*}
	Highly specialist (n=11)	123.8(21.6)^{b***}	50.7(20)^{ab**}	8.7(2.3)^{ab*}

2.3.3. Traits governing population trends of UK migrant passerines

Mean change in arrival date, average laying date and the average first clutch laying period were retained in the final best-fitted model and explained a significant amount of the variance in observed growth rates between migrants (Table 2.4a). Amongst these, mean change in arrival date was the most important predictor causing the largest drop in AIC_c (Table 2.4b) closely followed by average first clutch laying period. The coefficients for the phenological predictors indicated that population growth rates were higher in

species that had advanced their arrival date and have longer laying periods that begin earlier in the season (Table 2.4b). For the migrant species model, the mean change in arrival date made the largest contribution (54.4%) to the variance explained by the model closely followed by the average first clutch laying period (39.3%). Average laying date made the lowest contribution (6.2 %; Fig 2.2b).

Table 2.4. Population trend model for 14 UK passerines migrants based on life-history, phenological and resource use traits: a) Model performance for global, null and final models of population trends in migrant species. b) Predictor contribution and performance for best model. Δ AIC_c was calculated by removing each predictor from the model and calculating the difference in AIC of this model and the final model.**.** ****<0.001; *** 0.001<p<0.01; ** 0.01<p<0.05; * p~0.05

a)

Model	Variables included	Adj D^2	AIC_c	∆AICc
Null	-	0	64.08	11.39
Global	*As* Final + *Productivity+ Average body weight +Mean distance*	0.778	67.27	13.86
Final	*Average laying date+ Mean change in arrival date+ average period of 1st clutch laying*	0.824	53.41	-
Phylogenetic	*As* Final		68.29	14.88

b)

Explanatory variable (Best model)	Coefficient(SE) GLM	∆AICc	% times selected in bootstrap models
Mean change in first arrival date	12.05(2.3)****	14.9	95
Average period of 1st clutch laying	0.13(0.03)***	10.5	95
Average laying date	0.079(0.038)*	1.5	71

2.4 DISCUSSION

These analyses demonstrate that life-history traits, migration, phenology and resource use are associated with long-term population trends in UK passerines. Resource use, both habitat and diet, together with average 1st clutch laying period were strong predictors of population trends, suggesting that species able to utilise a wide range of resources and alter their phenology may be better buffered against environmental change, particularly in seasonal habitats (Both et al., 2010). Phenology and phenological flexibility was particularly important for migrants. Resident species are exposed to local climate conditions throughout the year, while long-distance migrants encounter conditions in their breeding range only after returning from over-wintering grounds. Thus the former have more, as well as better, cues to match their phenology to the changing environment (Végvári et al., 2009), which is supported by earlier laying dates in resident and partial migrants species (Jenni & Kéry, 2003; Rubolini et al. 2007).

The potential for migrant species to change breeding periods will be influenced by their ability to shift their migration timing appropriately. In most long-distant migrants, the spring arrival date is dictated by an endogenous rhythm based, in most cases, on changes in photoperiod (Dawson, 2008) though it has been suggested that climatic conditions on their journey to the breeding grounds may also impact species' ability to adjust their phenology (Moussus et al., 2010). The fact that mean arrival date was the most important contributor to the best-fitted model for migrant species suggests that this timing is critical. However, long-distance migrants will have fewer relevant environmental cues than resident or short-distant migrant species (Møller et al., 2008). Thus, phenological responses through changes in laying dates will be greatly constrained by the onset of their spring migration and ultimately arrival date (Lehikoinen et al., 2004). However, it seems that even with these intrinsic limitations, migrants are still able to modify their breeding phenology to somehow buffer for the limited

breeding period, as migrants with longer laying periods and advanced arrival dates were less likely to have declining populations.

The positive association between longer reproductive periods and population trends complement those of Møller et al. (2008, 2010), Végvári et al. (2009) and Van Turnhout et al. (2010) who demonstrated that advanced laying date allows species to respond better to climatic change (particularly warming of spring temperatures). They found that long-distance migrants advance spring migration-date the least and that species laying larger clutches showed the greatest advance in the timing of spring migration. A longer laying period may allow re-laying in the event of brood failure or allow for an extra clutch under good conditions. Previous studies have highlighted complex interactions between phenological and life-history traits (Jenni & Kéry, 2003; Rubolini et al., 2007; Moussus et al., 2010). Species which can shift their phenology to match optimal food availability will be more likely to invest their efforts into producing one single, larger brood. In contrast, species unable to track changes in their environment may show phenological flexibility, but may try to compensate by having multiple clutches (Crick et al., 1993; Visser et al*.,* 2003). However, in both cases the ability of species to respond appropriately may be restricted by an intrinsic limitation on clutch size increases (Winkler et al*.*, 2002). As a final point, it has also been suggested (Visser, 2008) that species will be selected for adaptability to changes in photoperiod that may allow migrant species to reduce their migration distances and therefore winter in areas closer to their breeding grounds where they could better assess changes in environmental conditions there, and ultimately change the timing of their phenological events to allow them to respond accordingly.

Besides the key role of phenological flexibility buffering against declines, we also confirmed that specialized habitat and diet requirements may render species more vulnerable to declines (Both et al., 2004; Jiguet et al., 2007, 2009). Of all the traits we evaluated, both habitat preference and diet type showed the strongest association with population trends. In terms of habitat

characteristics, wetland species generally showed stable or increasing population trends which may be associated with increased protection from disturbance and the creation of wetland reserves as a result of both British and European legislation (Ramsar Convention Secretariat, 2006). Generalist species and upland species appear to fare better than farmland, woodland or urban species. Previous studies have suggested that agricultural intensification, loss of hedgerows, increasing use of chemical products (fertilizers and pesticides) and changes in crop and ploughing systems have negative impacts on survival and fitness of farmland species during the wintering period, influencing species pre-breeding conditions (Chamberlain et al., 2000; Gregory et al., 2005; Wilson et al., 2009). Though the food resources may be more stable and readily available in agricultural habitats, particularly with the establishment of environmental stewardship schemes, the negative impacts of agricultural intensification may outweigh the positive effects of these new management measures (i.e. the introduction of wild bird seed mixture), particularly in the case of resident species (Natural England, 2008). The fact that farmland species are more vulnerable may indicate that their habitat quality is decreasing globally through fragmentation and land use change (Devictor et al., 2008). Population declines in woodland species are related to both woodland maturity and reduction in active management (Amar et al., 2006) and climatic changes such as changes in winter temperature (Leech & Crick, 2007). In addition, since most of the woodland species in our study are specialist or invertebrate/insect eating species (11 out of 14) and migrant (8 out of 14), their decreasing population trends may also be explained by the increased mismatch between key reproductive period and the peak of food supply (Leech & Crick, 2007), particularly for migratory species. As explained above, threats to wild birds and biodiversity are currently monitored using population changes in indicator species from different breeding habitats (cf Gregory et al. 2009). Our finding that migration behaviour, habitat use and phenological flexibility have interactive effects on the ability of species to adapt to environmental change suggests that impacts on biodiversity may be better monitored using separate indicators for migrants and resident species.

It was predicted that additional life-history traits would be associated with species population trends. As indicated, species that reproduce more slowly may be expected to take longer to adapt to environmental changes, and thus be more likely to decline (Sandvik & Erisktad, 2008). Resident and partial migrant species had larger productivity than migrant species, which may indicate trade-offs between migration and reproduction. Specific-species traits may result in complex and potentially opposing responses to environmental conditions across the annual cycle which will need to be fully understood in order to be able to determine their ultimate effect on population trends (Jenni & Kéry, 2003).

Previous studies have linked broad features of range structure or resource use to inter-specific variation in ecological responses to environmental change (Møller et al., 2008, 2010; Végvári et al., 2009; Van Turnhout et al., 2010). These results not only confirm this but also highlight the importance of phenological characteristics and their interaction with other species traits (Moussus et al., 2010). These results also underscore the need for a multifaceted approach to understanding the mechanisms governing the differential impacts of environmental changes on species and show the relevance of interactions between phenology, habitat and resource-use characteristics when developing indicators.

Chapter 3 : Environmental drivers of current avian community composition community in the UK

Abstract

In this chapter I look at the three key environmental pressures thought to be driving ecosystem change in the UK (namely climate change, land cover, biotic stress and pollution) and their particular individual and synergic contributions in shaping the avian community patterns observed in recent decades. Also the role of spatial factors, including broad scale spatial gradients, across the UK is accounted for by means of spatial eigenvectors namely PCNMs variables. By identifying the dominant pressures acting at this scale and their impacts on the different avian groups, I evaluate whether the distribution of avian communities at this scale provides a valuable bioindicator of ecosystem responses to environmental change. Results indicate that the most significant impacts on the bird assemblages are those related to the combination of climate, land cover and pollution as it may have been expected at this large scale. However, the amount of overall variation accounted for was relatively small which may indicated there may be other variables that are having an important role but were not considered in this analysis. It is also worth noting the differences observed between avian groups in terms of driver's importance in particular between raptors, coastal birds and the other groups (i.e. passerines, passerine-like and wetland birds) which may indicate their use as indicators for different environmental conditions.

3.1 INTRODUCTION

The current paradigm is that species distributions are governed by climate on broad biogeographical scales (Turner et al., 1987; Parmesan, 1996), whereas land cover and spatial distribution of suitable biotopes determine species occupancy patterns at finer spatial resolutions (Benton et al., 2003). Climate will

for example control species distributions and abundances by imposing physiological constrains (Root, 1988) while habitats could provide limiting resources and microclimatic conditions where species interactions occur (Wiens, 1989; Estrada-Villegas et al., 2012). Climate change is therefore often assumed to be a major cause of species extinction (Rosenzweig et al., 2007), and climate variables may be the only environmental predictors included in species distribution models (Berry et al., 2002; Hamann & Wang, 2006; Randin et al., 2009) when in fact multiple abiotic and biotic drivers are known to interact to drive species ecological responses.

Direct drivers of ecosystem change have an explicit effect on ecosystem processes (Nelson et al., 2005) and normally produce a change in the ecosystem that can be identified and monitored (Ash et al., 2008). As described in the Chapter 1, the most important direct drivers identified in the UK ecosystems according to the National Ecosystem Assessment are: land use leading to habitat change, pollution and nutrient enrichment; overexploitation of terrestrial resources (harvest and resource consumption); climate variability and biological drivers such as invasive species (UKNAE, 2011).

Factors influencing patterns of diversity are usually a combination of environmental and geographical variables (Borcard et al., 1992) although their relative role and importance will change according to taxonomic group, spatial scale and geographic regions of the species under study (Xiu et al., 2012). Many studies have revealed the existence of relationships between species and their environment at multiple scales (Xiu et al., 2012; Estrada-Villegas, et al., 2012) but few have used methods that explicitly account for the spatial structure of data (Titeux et al., 2004; O'Hare et al., 2012). Recent advances in spatial data and ecosystems modelling for the UK (e.g. LCM, FRAME) now allow spatial proxies of most of the direct drivers of biodiversity change to be considered in national scale models of species and community responses. This then builds on the work of prior studies of avian communities where particular drivers have been neglected and may give a misleading impression of the

importance of, and sensitivity of avian indicator groups to climate drivers (Araujo et al., 2005; Schwartz et al., 2006; Peterson, 2003).

Analysis and modelling of species-environment relationships present many statistical difficulties. First, multicolinearity between explanatory variables can hamper the detection of key environmental factors underlying species environment relationships identified by traditional regression approaches (MacNally, 2000). Second, spatial autocorrelation of the data violates the assumption of independence of most standard statistical procedures and can lead to pseudoreplication (Legendre, 1993). Third, species interactions are normally ignored in most single species models though it has been shown that the presence of other species in the environment significantly alters species distributions (Araujo & Luoto, 2007; Heikkinnen et al., 2007).

In order to explain relationships between species locations and environmental variables, multivariate ordination and community approaches are often used to directly relate species occurrence to environmental variables (ter Braak, 1986; Titeux et al., 2004). Since these approaches allow for the study of a variety of species and predictors simultaneously, they provide for interpretations and results that are not possible with single species methods (James, 1990). For example, by incorporating a number of species, theoretically it would be possible to inherently account for the effect in species distributions due to biotic interactions within their community. Also multivariate methods can incorporate procedures to deal both with predictor multicollinearity and spatial autocorrelation. Multicollinearity arises from the inclusion of large number of predictors that present similar geographical patterns which could hinder analysis by overestimating the amount of explained variance in a model. In order to avoid this, procedures to select the most adequate predictors can be implemented. For example, Blanchet et al (2008) have proposed a method easily integrated in both regression and canonical redundancy analysis that allows for the forward selection of explanatory variables and therefore helps deal with issues related to predictor multicollinearity.

Apart from multicollinearity, spatial autocorrelation is a major issue in modelling species distributions and their relation to environmental variables. The differentiation between environmental and geographical spatial structuring will be fundamental to accurate description of species-environmental relationships (Legendre & Legendre, 1998; Titeux et al., 2004). Appropriate methods dealing with this very general property of ecological variables exist (Legendre & Troussellier, 1988; Borcard & Legendre, 2002; Legendre et al., 2012). Borcard & Legendre (2002) proposed the use of eigenvalue decomposition of a truncated matrix of geographic distances among the sampling sites (i.e. principal coordinates of neighbour matrices, PCNM). These spatial variables are orthogonal and they represent the spatial variability present in the geographical space at different scales (Borcard & Legendre, 2002). Once they are calculated, they can be integrated into models to help account for spatial structures unrelated or unaccounted for by the selected environmental predictors.

Another advantage of ordination methods is their development of a variance partitioning framework, where ecological variation can be decomposed into different fractions (i.e. pure environmental, pure spatial, explained both by space and environment, and unexplained) and their relative role in driving the observed patterns in the species data can be simultaneously assessed (Borcard et al. 1992; Borcard & Legendre, 2002).

The degree to which environmental or spatial factors will be associated with the species variation in a community structure will also vary as a function of the characteristics of the community under study and the characteristics of the constituent species (Burgess et al., 2010). Different species might experience and utilize habitats in different ways and at different scales, according to their perceptive ability and their characteristic home ranges (Belmaker and Jetz, 2010). Few studies have examined communities of very different taxonomic groups from the same environment and the differences in the factors or mechanisms controlling the composition of these communities over similar

scales (Connolly et al., 2005; Burgess et al., 2010). With not many studies integrating the environmental (i.e. climate, land use, pollution, biological factors) and spatial components potentially influencing organisms, it is difficult to understand the factors driving species diversity, abundance and community composition. Furthermore, it would be fundamental to understand these interrelations to better predict and mitigate the responses of organisms to human-induced perturbations such as changing land use, pollution and climatic changes (Yergeau et al., 2010).

The aim of this study, therefore, was to distinguish the effects of different environmental drivers of the UK avian community composition namely: climate, land cover, pollution and biological factors using an ordination modelling approach that accounts for the spatial structure of the data. Furthermore, I examined whether impacts of drivers on broad functional or taxonomic groupings of birds differed from the whole avian community and whether community models were more accurate for a particular group. Finally, these results were assessed in terms of the suitability of such avian groups as bioindicators of different kinds of environmental change.

3.2 Methods

3.2.1.Species data

Data for 212 UK bird species was extracted from the 2nd Breeding Bird Atlas of the British Isles (Gibbons et al., 1993). As land cover data was not available for Ireland, all Irish squares were excluded; here for convenience the geographic study area is referred to as Britain and includes all islands where data were available. The field work for this survey took place between April 1st and July 31st in each of the four years 1988-1991. Observers visited a minimum of eight tetrads (2x2 km square) of their own choice within each 10x10 km square. Two hours were spent in each tetrad and a species list was compiled for each. It was recommended that the two-hour period be split into two hour-one visits, one

early in the season (April to May) and one late (June to July) to ensure that summer migrants were assessed. The frequency of occurrence (=frequency index) of each species in each 10x10 km square was expressed as the proportion of tetrads visited in which the species was found (Gibbons et al., 1993). The results of a pilot survey undertaken in 1987 showed that such indices were correlated with a measure of absolute density, although strictly they reflect how widespread a species is within in a given 10km square (Gibbons et al., 1993). Here, the frequency of occurrence of all the species in the community within each 10 x 10 km square was used as the response variable.

Species were grouped into five (Table 3.1), based on taxonomic order and general shared ecological characteristics (see Appendix B for full list of species and orders). The passerine group consisted of species within the Passeriforme order; passerine-like birds included orders that either through ecological characteristics or life history traits (i.e. body size) could be considered as competitors with passerine or similar species (e.g. woodpeckers, pigeons, cuckoos); coastal birds were mainly orders/species associated with coastal areas/habitats; wetland birds included species linked to both natural or artificial wetland areas, and finally the raptor group included orders with bird species that could be considered as predators of smaller species such as passerines or passerine-like species (e.g. eagles, kites, etc).

Table 3.1 Avian groups by species order used to structure the community analysis; the grouping of species was based on taxonomic and ecological traits.

Group	Passerines (n=87)	Passerine-like (n=11)	Coastal birds (n=47)	Wetland birds (n=32)	Raptors (n=20)
Orders included	Passeriformes	Coraciiformes Piciformes Columbiformes Apodiformes Cuculiformes	Charadriiformes Pelecaniformes	Gruiformes Anseriformes Ciconiiformes Podicipediformes	Strigiformes Accipitriformes

3.2.2. Environmental data

Environmental predictors were abstracted from a number of sources (Table 3.2) and rescaled to the resolution of the species data; these variables were grouped into abiotic, biotic and spatial sets, with the abiotic set being split into climatic, land-use and anthropogenic sub-sets (Table 3.2). Decadal (1980-1990) climatic data (i.e. temperature, precipitation and growing season length) was acquired from the UK Climate Impacts Programme (UKCIP) section of the met office database (http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/). Monthly average values of minimum, maximum and mean precipitation and temperature were calculated across the decade and then averaged across different stages considered to be important in the life cycle of birds (such as early/late breeding or nestling period) (see Table 3.2). Land-use data was extracted from the Land Cover Map 1990 (1km^2 resolution, http://www.ceh.ac.uk/LandCoverMap1990.html) and the mean cover of each respective class (e.g. arable, coastal, coniferous forest, etc…) in each 10km grid cell calculated (see Table 3.2). Air pollution concentrations were obtained from the FRAME project (http://www.ceh.ac.uk/sci_programmes/EMEP4UK.html); these data represent air concentrations of the main pollutant compounds in 1990 (see Table 3.2). For biological data, cattle and sheep densities were extracted from the agcensus database at 2km resolution for the 1988 (http://edina.ac.uk/agcensus/) and their densities calculated for each of the 10km grid cells (see Table 3.2). Human population data was extracted from the 1991 census (http://cdu.mimas.ac.uk/1991/index.htm) (see Table 3.2).

3.2.3.Principal coordinates of neighbour matrices

Spatial predictors were calculated using two methods using British national co-ordinates, i.e.: (1) principal coordinate analysis of neighbour matrices (PCNM) and (2) multi-scale pattern analysis (MSPA). Several approaches have been proposed to introduce space into ecological models in order to identify or to

remove the effects of spatial processes. PCNMs are uncorrelated variables decomposing the spatial variability into different, but complementary scales (Borcard & Legendre, 2002). They are particular cases of eigenvectors of a spatial weighting matrix which are used to remove spatial autocorrelation from residuals of a model so that standard statistical tools can be used. PCNMs can serve as spatial predictors in constrained ordinations. This analysis yielded 1250 PCNM eigenvectors (~ 2n/3 where n is 2520 sites) with positive eigenvalues, reflective of positive spatial autocorrelation for use as spatial predictors in multivariate analysis. The analysis was further restricted to those PCNM eigenvectors that represented statistically-significant spatial autocorrelations according to Moran's I (p-value <0.05). The MSPA ordination method uses Moran's eigenvectors maps (MEMs) to decompose ecological variability into several spatial scales and then summarizes this decomposition using graphical representations (Jombard *et al*., 2009). The canonical form of MSPA can also be used to assess the spatial scales of the species-environment relationships. Both calculations were implemented in the package ade4 under within the R statistical environment (http://CRAN.R-project.org), and since they yielded similar results, only the PCNM analysis is reported here.

Table 3.2. Environmental predictors used in the community analysis of avian communities in Britain.

Driver group	Predictors	Variable details
Climate (12)	Temperature min.	Early breeding (Mar-May), Total breeding period (Mar-Aug), Nestling period (May-Aug), February(~pre-breeding conditions), October(~post-breeding conditions)
	Temperature max.	Late breeding (Jun-Aug), Early breeding (Mar-May, Nestling period (May-Aug)
	Precipitation	Early breeding (Mar-May), Total breeding period (Mar-Aug), Nestling period (May-Aug)
	Growing season length	-
Land use (9)	Land cover map 1990	Mean cover of: arable, coastal, coniferous forest, decideous forest, grassland, estuary, shrubland, suburban, wetland
Pollution (8)	Air pollutant concentrations	NO3 , HNO3 , PM10 , NH4, SO4 , SO2, NOx, NH3
Biological (3)	Cattle and sheep Human population	Total numbers from *agcensus* Census data 1991
Space (50)	PCNM vectors	50 first PCNM vectors

3.2.4.Statistical methods

In order to determine the most appropriate ordination method to use in this study, Detrended Correspondence Analysis (DCA, ter Braak & Smilauer, 2001) was carried out on the species dataset. Initial inspection of the results produced eigenvalues of 0.341, 0.117, 0.064 and 0.045 and gradient lengths of 3.193, 3.06, 2.591, and 1.522 for the first four axes respectively. Considering the scale of the analysis and that the gradient lengths for the first two axes were closer to 3, an unimodal ordination method was considered appropriate (e.g. Correspondence Analysis (CA) and Canonical Correspondence Analysis (CCA), ter Braak & Smilauer, 2002). CA is an ordination technique for investigating the separation of species niches or the ecological amplitudes of species. Ter Braak (1986) further developed CCA explicitly devoted to niche separation along environmental gradients (Dolédec *et al*., 2000). CCA was especially designed to

extract the best combination of environmental variables (synthetic gradient) that maximizes the variance of the weighted average species positions ("niche centroids") (Dolédec *et al*., 2000). In addition, CCA implies that the importance of environmental measurements is proportional to the number of individuals per site.

Forward selection of explanatory variables

One of the major problems faced by ecologist when investigating why species and communities are structured is the large number of correlated environmental variables available (Blanchet et al., 2008). Hence there is a need to select a subsample of these factors that explain the most amount of variance hence allowing for the development of a parsimonious model that has greater predictive power (Gauch 2003; Blanchet et al., 2008).

Forward selection has been the most used method to select the most appropriate variables within a dataset. It presents the great advantage of being applicable even if the initial data set contains more explanatory variables than sites, which is often the case in ecology (Blanchet et al., 2008). However, it is well-recognised that classical forward selection overestimates the amount of variance explained and inflates the Type I errors. Therefore, in this study, we applied a corrected forward selection procedure as presented by Blanchet et al. (2008).

Before applying this method, we used the variance inflation factors (VIFs) and correlation values within each environmental sub-set (Table 2.2) to explore variable correlation levels and those predictors with high values (VIF>10) were excluded from further analysis. Forward selection was then run within each set to optimize the model fit and to select those variables that explained the most variance in the dataset. Following the methodology outlined in Blanchet et al. (2008) forward selection was only carried out on the predictor set if a global test using all explanatory variables was significant. Thereafter, to prevent over-estimation of variance explained by a given predictor set, two stopping criteria

were used: (i) an alpha significance level of 0.05 with p-values (*P*), obtained from permutation tests (n=9999), corrected after Sidak (1967) for the number of tests, where $P_s = 1-(1-P)^k$ where *k* was equivalent to the number of variables in the predictor set, (ii) the adjusted coefficient of multiple determination (R^2_a) of the global model with all explanatory variables (see Blanchet et al. 2008 for further details). This procedure was repeated for the overall and each bird group dataset.

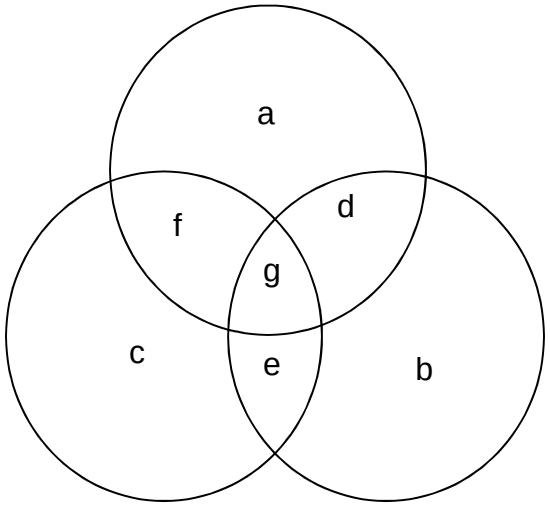
Variance partitioning

As delineated in Borcard et al. (1992), variance partitioning allows for the measurement of the relative contribution of sets of explanatory variables by using eigenvalues of constrained and partial ordinations. This concept is conceptually linked to the idea that ecological phenomena are explained by non-mutually exclusive processes that overlap in space and time (Borcard et al. 1992) which allows for the quantification of the total percentage of variation explained into unique and common contributions of the sets of predictors (Borcard et al., 1992). Hence, the relative role of climate, land cover, pollution, biological and spatial factors in driving avian communities was evaluated using a variance partitioning technique where the total percentage of variation explained by a Canonical Correspondence Analysis (CCA; Legendre and Legendre 1998) is partitioned into unique and common contributions of the sets of predictors (Borcard, 1992).

This was done for both the overall species dataset and for each of the established avian groups to compare any significant differences in predictor impacts.

Variance partitioning for CCA was done using the outlined sets of predictors (i.e. land cover, climate, pollution, biological and spatial data) divided into different subgroups to facilitate the analysis (i.e. climate, land use and pollution were initially grouped into one single category of environmental drivers). Of the eight fractions that can be calculated in a set of three variables(Fig 3.1), three

can be directly obtained from partial CCAs and correspond to the independent effects of those factors (a, b and c in Fig 3.1). The remaining fractions are calculated on the basis of more than one canonical analysis as the joined effects of couple of factors (d, e and f in Fig 3.1) or the combined contribution of all factors (g in Fig 3.1). Also the amount of unexplained variance can be calculated as 1 minus the sum of fractions (h in Fig 3.1).



[h]

Figure 3.1. Diagram describing partition of variance fractions

Analogous to multiple regression, the amount of explained variance in CCA or redundancy analysis is influenced by the number of explanatory variables as well as the sample size (both number of sample sites and species in this examples) (Peres-Neto et al., 2006). Hence in this study we applied the variance partition procedure outlined in Peres-Neto et al., (2006) where coefficients of determination where adjusted for the numbers of predictors in each set of environmental variables. This adjustment, as previously noted, is not only preferable but necessary to provide more accurate estimations and valid comparisons between set of factors when explaining community structure (Peres-Neto et al., 2006). Significance of fractions was tested by permutation tests (n=9999) (Borcard, 1992).

3.3 RESULTS

3.3.1.Avian community composition

The first two axes of the overall CCA analysis produced eigenvalues of 0.292 and 0.103, and they explained 19% of the total observed variance (Fig 3.2a). Axis 1 represents a gradient from lowland communities with high anthropogenic influence (-ve) to upland more natural ones (+ve). The lowland areas are correlated with increasing maximum temperatures in late summer, high aerial pollution and arable land use, while upland areas are associated with colder late summer conditions, less polluted areas and shrubland (Fig3.2a). Axis 2 represents a gradient of temperature-precipitation from mild dry winters (-ve) to colder wetter ones (+ve), essentially a south-north axis. Also there is gradient from more pastoral areas (dominated by sheep farming) (+ve) to more arable land-uses (-ve) (Fig 3.2a).

The highest diversity of species was correlated with warmer, drier climates and with man-managed habitats (arable). Species numbers declined (1) with decreasing temperatures and increasing precipitation (northerliness) and this was also correlated with increasing shrubland cover (Fig 3.2a).

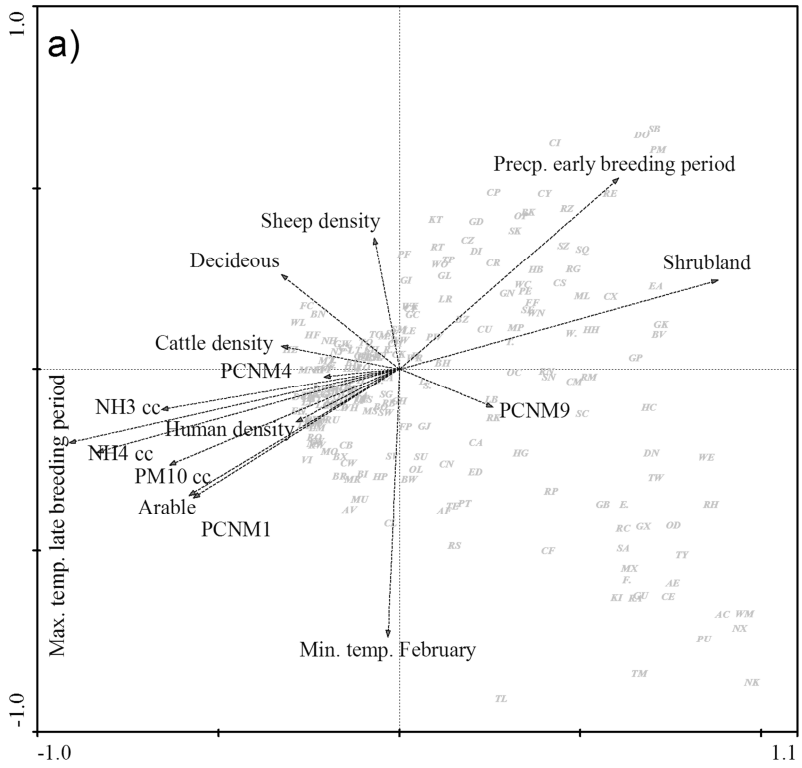


Figure 3.2 CCA analysis of the avian community of Britain. Arrows represent significant environmental variables used in the analysis. For species codes see Appendix, supplement B.

The ordination reveals that the majority of avian groups overlap in the environmental space they occupy without any clear environmental separation (Fig 3.3). Passerine-like species are mainly concentrated in areas characterized by a significant anthropogenic influence (i.e. areas with high human density, arable areas and those with significant nitrogen loads) while the other groups appear more randomly distributed along both ordination axes (Figs 3.2 and 3.3). Raptors appear to spread out mainly along axis 1 from arable sites towards more open shrubland land-uses (Figs 3.2 and 3.3). Meanwhile wetland and coastal species seem to spread mainly along axis 2 along the temperature-precipitation gradient (Figs 3.2 and 3.3).

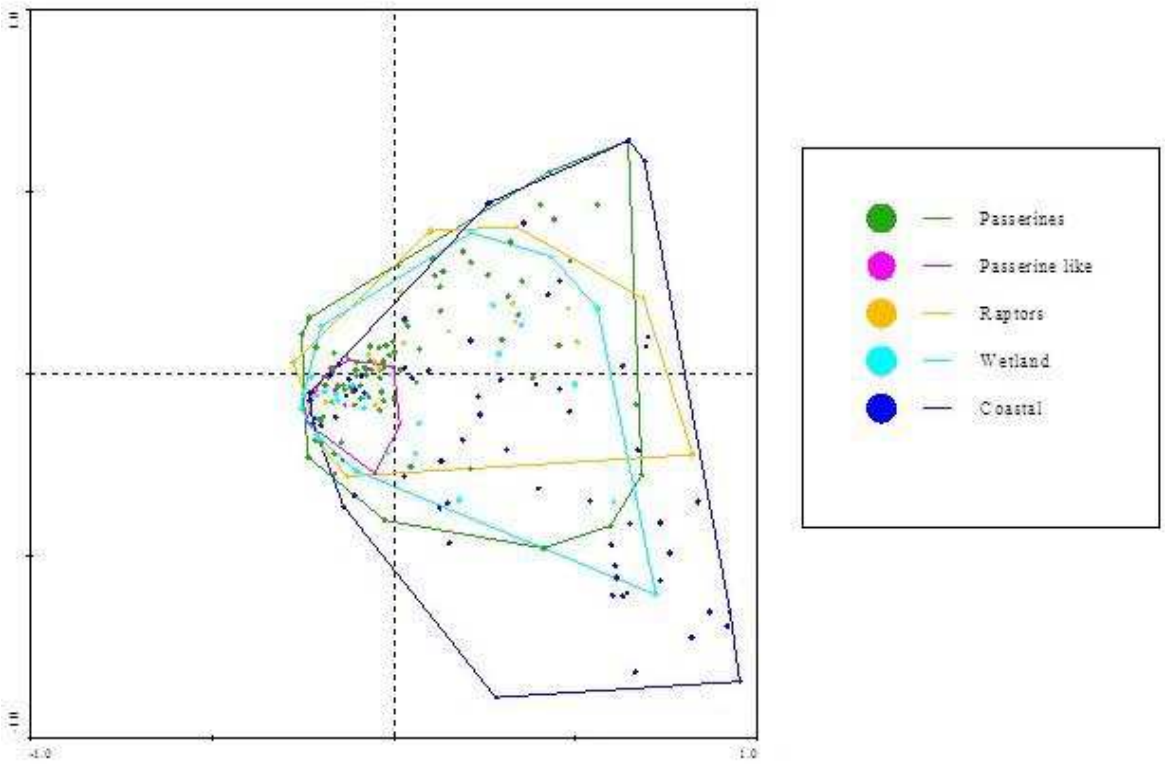


Figure 3.3 CCA biplot of the avian community of Britain grouped by bird groups.

3.3.2.Identification or the most important environmental of drivers of avian community composition in Britain

The main drivers of the bird community in the UK selected using forward selection appear to be quite similar among species groups (Table 3.3). The maximum temperature during the late breeding period (June-August) was the main climatic predictor, with percentage of shrubland/ arable land as the main land cover variables for all groups except the coastal species, cattle density was the only biological variable selected, NO_3 concentration was the main pollution predictor and PCNM1 was the main spatial vector for all groups except raptors where it was PCNM3.

At this scale the main spatial vectors represent broad-scales such as north-south, east-west gradients (PCNM1and PCNM9 respectively, Fig 3.2a).

However, finer grained spatial vectors were also significant representing a more heterogeneous pattern around the coastal areas (e.g. PCNM28, Fig 3.2).

Table 3.3 The top three environmental variables that explained significant variation in community composition of avian species in Britain; CCA analyses are presented for all species and for individual species groups. Among all the studied predictors the most important in terms shaping the avian community in the UK appeared to be: climate (Late breeding maximum temperature, early breeding precipitation and February minimum temperature), land cover (Shrubland, arable lads and deciduous woodland), pollution (NO_3, NH_3 and PM10), biological pressure (cattle density, human density and sheep density) and spatial structure (PCNM1, PCNM3 and PCNM 9).

		Bird grouping					
		All species	**Passerines**	**Passerine-like**	**Raptors**	**Wetland birds**	**Coastal birds**
Climate	**1**	Late breeding max temp.	Late breeding max temp.	Late breeding max temp.	Early breeding precp.	Late breeding max temp.	Late breeding max temp.
	2	Early breeding precp.	Early breeding precp.	Early breeding precp.	Growing season length	Early breeding precp.	Early breeding precp.
	3	February min. temp.	October min. temp.	Total breeding max. temp.	Nesting max. temp.	February min. temp.	February min. temp.
Land cover	**1**	Shrubland	Shrubland	Shrubland	Arable	Arable	Estuary
	2	Arable	Deciduous	Arable	Shrubland	Shrubland	Shrubland
	3	Deciduous	Arable	Deciduous	Suburban	Estuary	Deciduous
Pollution	**1**	NH4 cc	NO3 cc	NO3 cc	NO3cc	NO3 cc	NO3 cc
	2	NH3 cc	NH3 cc	PM10 cc	NH3 cc	SO4 cc	PM10 cc
	3	PM10 cc	PM10 cc	NH3 cc	PM10 cc	PM10 cc	HNO3 cc
Spatial structure	**1**	PCNM 1	PCNM 1	PCNM 1	PCNM 3	PCNM1	PCNM 1
	2	PCNM 4	PCNM 4	PCNM 3	PCNM 7	PCNM 3	PCNM 28
	3	PCNM 9	PCNM 9	PCNM 9	PCNM 1	PCNM 9	PCNM 18
Land use intensity	**1**	Cattle density	Cattle density	Cattle density	Sheep density	Human density	Cattle density
	2	Human density	Human density	Human density	Human density	Sheep density	Human density
	3	Sheep density	Sheep density	Sheep density	Cattle density	Cattle density	Sheep density

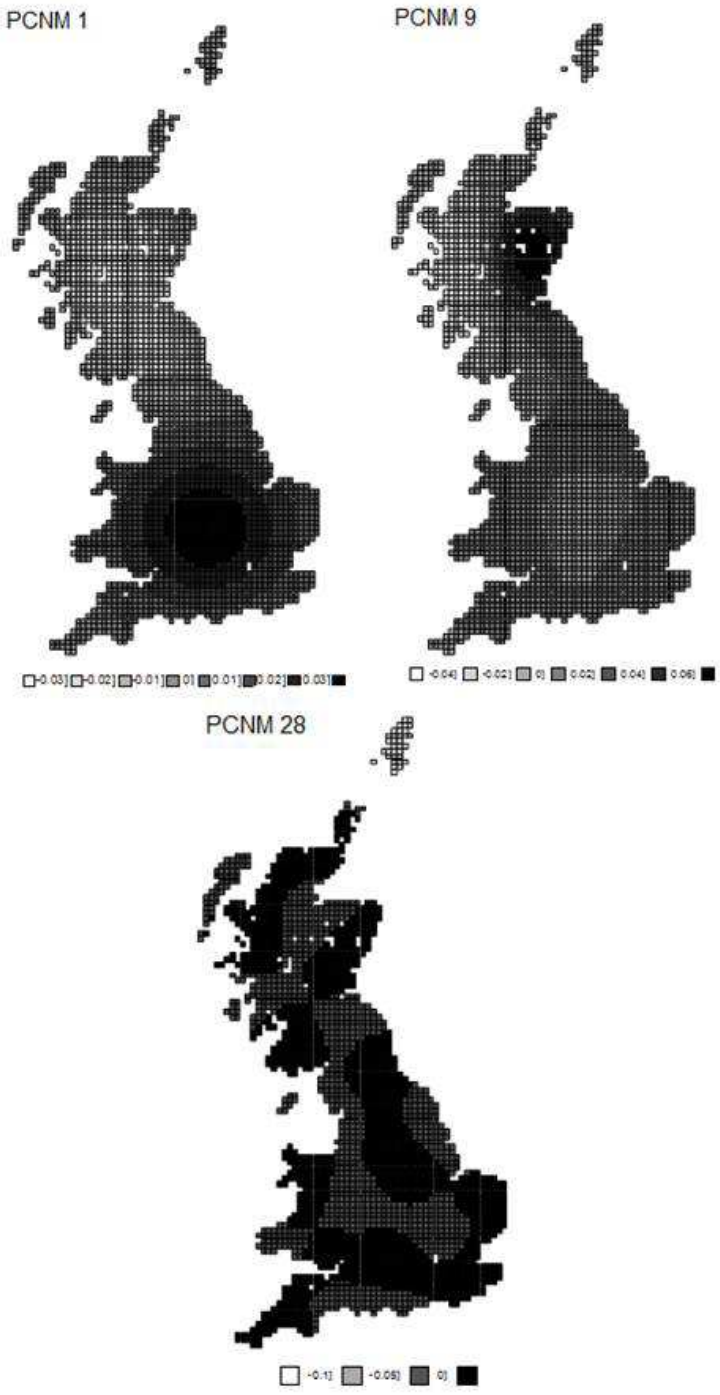


Figure 3.4. Principal coordinates of neighbour matrices (PCNM) vectors of avian community composition in Britain. These PCNM vectors describe variable degrees of possible spatial structure with lower vectors representing regional-scale groupings and higher order vectors representing more local-scale groupings. Colour represents the sign (- white, + black).

3.3.3.Assessing the relative importance of the environmental of drivers of avian community composition in Britain

The overall variation explained by the measured environmental variables was ca. 49% for all species together, while the models for each individual group were as follows: for both the passerine and passerine-like species 52% and between 34% and 40 % for raptors, wetland and coastal species (Table 3.4a). Most of this explained variation could be attributed to climate, land use and pollution on their own (ca. 20%), or shared variation between these predictors and special variables. Almost no variation was attributed to biological variables on their own, except for a small amount in the case of the raptors (2%) and very little was ascribed to spatial variables on their own (< 5%). Decomposing the fractions for climate, pollution and land use variables in a similar manner (Table 3.4b) the levels of total explained variance were slightly lower (47% all species, ca.50% for passerines and passerine-like; 30-35% for raptors, wetland and coastal groups). The amount of variance explained by single variables ranged between 1-8%, with the largest portion being explained by land cover (although for coastal species climate was equally important) (Table 3.4b). The main contribution was due to the joined effects of the three drivers though values varied considerably amongst groups (i.e. passerine and passerine-like 27-28%, raptors 7%, coastal 11% and wetland 18%).

Table 3.4. Variation partitioning results illustrating the relative importance of (a) climate, land use and pollution vs biological and spatial sets, and (b) climate, land use and pollution in explaining avian communities in Britain.

a)

Environmental drivers	% Variance explained in avian group					
	Passerines	Passerine -like	Raptors	Coastal	Wetland	All
Climate+Land Use+Pollution	21	21	21	24	17	21
Biological	0	0	2	0	0	0
Space	2	1	2	3	1	2
Climate+Land Use+Pollution + Biological	5	4	5	2	3	4
Biological+Space	0	0	0	0	0	0
Space+Climate+Pollution+Land use	16	20	4	8	10	16
All	8	6	0	3	3	6
Residuals	48	48	66	60	66	51

b)

Environmental drivers	% Variance explained in avian group					
	Passerines	Passerine -like	Raptors	Coastal	Wetland	All
Pollution	1	2	4	2	1	2
Climate	3	3	4	7	2	4
Land cover	8	7	6	7	5	8
Pollution+climate	1	4	1	2	2	2
Pollution+Land cover	2	2	4	1	2	2
Land cover+Climate	7	4	3	7	3	6
Pollution+Climate+Land cover	27	28	7	11	18	24
Residuals	50	49	70	63	67	53

3.3.4.Avian grouping responses to main environmental of drivers

In this study species richness showed a distinctive response to the different environmental pressures between avian groups (Fig 3.5). In general, passerines, passerine-like and, to a certain extent, wetland species exhibit similar patterns for all drivers under study while for coastal and raptor species the response curves were notably different (Fig 3.5).

In terms of climate, temperature (i.e. late breeding maximum) appeared to have a positive effect on passerines, passerine-like and wetland species numbers with increasing the proportion of species present as temperature rises, whereas the opposite was true for coastal birds and an minor increases were observed in raptors numbers (Fig 3.5a). With regards to precipitation, again, passerines, passerine-like and wetland species presented similar trends in species proportions with decreasing numbers as precipitation increased (similar for raptors but at a smaller scale) and in coastal appeared to increase with intermediate precipitation levels (Fig 3.5b).

The main two land covers selected seemed to have opposite effects on the studied avian groups (Fig 3.5c,d). While increasing arable land appeared to have a slightly positive effect on proportion of passerines, wetland and passerine-like groups, shrubland had the opposite effect (Fig 3.5c,d). In the case of coastal birds, increasing arable land had a negative effect while shrubland had a positive effect (Fig 3.5c,d). Finally for raptors the amount of arable land appeared to have no notable effect on their richness while shrubland had a negative effect (Fig 3.5c,d).

Finally, regarding pollution (i.e. NO3), higher concentrations had a positive effect on the proportions of passerine, wetland and passerine-like groups while it reduced the number of coastal birds and for raptor a slight increase in richness was observed at medium concentrations (Fig 3.5e).

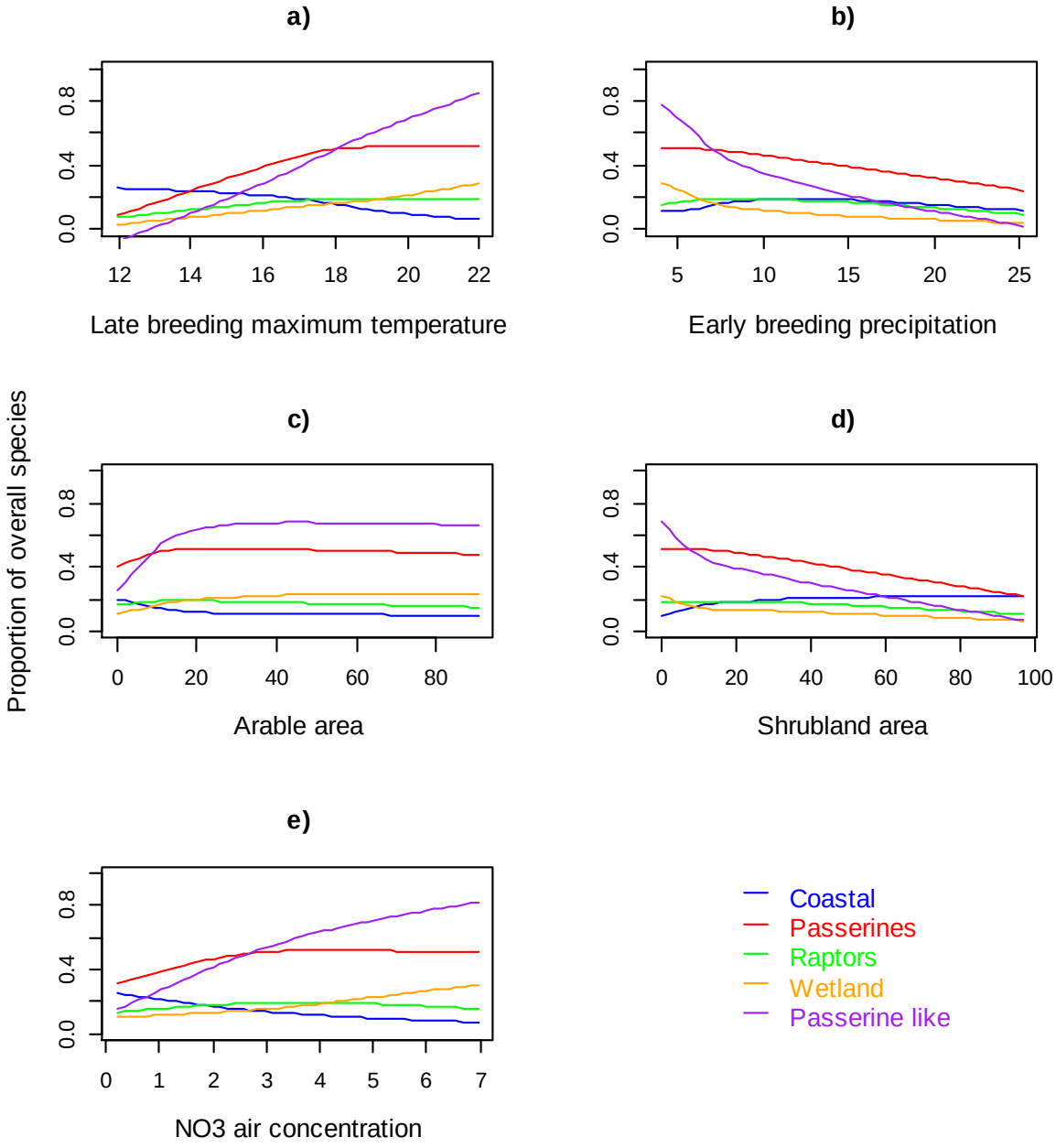


Figure 3.5. Response curves for each avian group in terms of the proportion of the total number of species present in relation to significant environmental drivers identified in the analysis: a) Maximum temperature during late breeding period; b) mean precipitation during early breeding period; c) area of arable land; d) area of shrubland and e) air concentration of NO_3 .

3.4 DISCUSSION

This study combines community modelling approaches with spatial data on a wide range of drivers to disentangle the influence of different environmental factors including climate and land use on avian communities in the UK.

As mentioned in Chapter 1 the most important direct environmental drivers are land use change, pollution, biological drivers and climate (UKNAE, 2011). These are known to affect species distributions although as mentioned in the introduction this will depend on the study group, the spatial scale amongst others. In this study dominant pressures on all avian groups were observed to be interactive effects of climate, land cover and pollution. This is not surprising as it has already been reported that most environmental factors act in combination, with changes in climate affecting the impacts of land cover (Kivinnen et al., 2007; Eglinton & Pearce Higgins, 2012) or increases in pollution altering the influence of land cover (Matson et al., 2002). For example Kivinen et al (2007) point out that trends of butterfly species in boreal agricultural areas are influenced by both climate and habitat availability with increasing populations in areas of favourable climate and suitable habitat available. Considering the rapid changes in these environmental drivers in the UK over the pass decades: more intense, large-scale and specialized farming, high level of livestock on uplands coupled with higher levels of pollution deposition, climate variability, etc…Interactions between these environmental variables could work to further modify the range of responses of species to individual drivers (de Chazal & Rounsevell, 2009). These interactions could work by exacerbating the effects of each other like for example species are more vulnerable to population declines through loss of habitat and poor climate conditions (Opdam and Wascher, 2004) or they could ameliorate the impacts as shown by Thomas et al. (2001) if for example increases in temperature allow species to expand to new areas that were unsuitable before.

Nevertheless, independent effects were also observed on our analysis. Land cover was in general the most important factor for all avian groupings, though the effect of climate and pollution was also important for coastal and raptor species respectively. The significance of land use as the main independent contributor to community structuring comes as no surprise. Previous studies have demonstrated the importance of land use, and land use intensity in particular, in influencing species populations. For example, Eglinton & Pearce-Higgins (2012) showed that despite the similar explanatory power between climate and land use intensity when measuring fluctuations in population trends of bird species, land use intensity was still the dominant driver. Even in this study, despite being at a scale that will be considered more appropriate to detect climate impacts (10 x10 km^2) the effect of land use seem more substantial. This could be explained by the fact that even though climatic changes have been reported such as higher temperatures, greater prevalence of hot days or more intense precipitation events (UKNAE, 2011) their impacts may be not as immediate as those of land use change. The UK land use is dominated by agriculture (with about 50% of the total land area of the UK used for agriculture either in form of grassland/rough grazing or crops/fallowland, DEFRA, 2008). Agricultural land management has intensified significantly since the end of the Second World War with increased use of chemicals and machinery per unit area (Rousenvell & Reay, 2009) and this not only shifted the balance between arable and pastoral land use but also resulted in the conversion of semi-natural habitats into farmland (UKNAE, 2011). All these changes mean that the availability of particular habitats that may be vital for species survival (in terms of habitat as shelter or areas to forage) have significantly changed over short time periods rendering land use the dominant environmental driver.

However, as it has already been established the response of different species to different drivers may be reliant on the characteristics of this species. In terms of this analysis we have seen that despite similarities in the amount of variance explained by the community models amongst groups there were also

substantial differences. While passerine birds were quite similar in response and driver importance to passerine-like species and wetland bird which may be explained by their similarity in resource use in terms of habitat, diet, range size and behavioural traits, there were notable differences with other two groups (coastal birds and raptors). In the case of coastal species the importance of climatic variables appear to be as important as land cover. This could be a spurious correlation that arises due to the inherent characteristics of coastal areas which tend to be milder climatically as compared to more inland areas or it could actually be due to the fact that this group is heavily dependent on other drivers that are not so important for inland birds. Seabirds are at the ecotone of terrestrial and marine habitats and therefore would be particularly sensitive to multiple and potentially synergistic climate variations (Sydeman et al., 2012). Coastal birds could be affected by warming of air temperature and changes of timing or intensity of precipitation that may affect their access to nesting colonies that could potentially increase mortality or indirectly affecting regional food webs or pelagic habitats (Sydeman et al., 2012). Hence this multifaceted effect of climate conditions on coastal birds maybe the reason why the climatic factors appear to be of more relevance to this group.

In the case of raptors the most striking aspect of the community models was their low explanatory power to explain the variance observed in the group. This may indicate that though these species may be using similar areas of the environmental space the factors having most influence in explaining their distribution are quite different and could be associated with the fact that they might be perceiving their environment in very different ways (i.e. reacting to different environmental variables from the other groups) and/or operating at different spatial scales (Cushman & McGarigal, 2002; Aviron et al., 2005; Sattler et al. 2010). For example, Sattler et al. (2010) investigated the importance of a set of environmental variables in shaping the communities of spider, bees and birds in different location and at different scales. Their study confirmed that bird species individually show variable reactions at different spatial scales according to specific ecological/ biological requirements (Sattler et al., 2010). Raptors in

general present large home ranges that are generally scarce which conflicts with the typical geographical scale of the other groups and in some cases have recently been on the process of population recovery from persecution and pesticide use (Amar & Redpath, 2004). As in the case of coastal birds, raptor species are at the top of food webs and any impacts or changes that affect the lower levels of the food chain will also indirectly affect this group. For example changes in farmland that have caused declines in common prey species such as granivorous birds or small mammals have also the potential to affect predatory species that rely on these land uses for hunting grounds (Amar & Redpath, 2004).

Though the main factors associated with structuring communities were taken into consideration still a large part of the variation observed was unexplained, particularly for raptors, coastal and wetland species. This could be due to the broad spatial scale of this study which could hinder the ability of the model to capture true effects of different environmental pressures. As it has been established before, different environmental drivers will be dominant at different scales and also their effects will be reliant of the species perception of environmental scale (Rojas-Ahumada et al., 2012). Hence, maybe the large unexplained variation could be just a result of the mismatching between the spatial resolution of the study and the species natural scale. Also as mentioned before, the low variance explained by the different models could be due to the omission of other variables that could be having significant impacts in the avian community. For example, even though different types of land use type were incorporated in the set of environmental drivers no direct measure of land use intensity was incorporated which could potential be of more relevance to avian population and community responses.

Another explanation for these moderate results in raptor, coastal and wetland communities could be that some of the habitats included in the analysis are poorly recorded or difficult to model (i.e. wetlands) hence the models do not perform as well for these habitat specialists (McPherson & Jetz, 2004).

On the other hand, models for passerines and passerine-like communities explained around 50% of the observed variance which for these types of community models is a fairly good result (Titeux et al., 2004). This could not only be due to the inherent characteristics of these groups to respond to particular environmental driver but may be also due to the fact that they are the most species rich group in the dataset causing the model to better describe their community and environmental space.

In terms of the use of these models to determine which avian groups would be better to monitor particular environmental drivers, taking into account the discussed limitations in previous paragraphs, it appears passerine and passerine-like species would be the most rounded groups in terms of responses to a wider range of environmental predictors and the higher percentage of variance explained by their models. However, considering the ecological characteristics of the other groups there could be a potential to use community responses of coastal birds to monitor climatic changes in marine ecosystems and potentially also raptors could prove useful in inspecting land use/intensity changes in selected habitats (e.g. farmland).

Chapter 4 : Changes in pressures on UK passerine community composition over time: a coarse scale method.

Abstract

Many passerine species are used as wild bird indicators of environmental change and ecosystem health in the UK. This taxa is ecologically very diverse and thus may be representative of a wide range of mechanisms of response to environmental change. In this chapter, I investigate how environmental pressures on passerine community composition may have changed in importance overtime in the UK, considering the relative roles of three key environmental pressures thought to be driving ecosystem change in the UK (i.e. climate change, land cover and pollution). I use spatial eigenvectors to account for spatial factors. Results from this study regarding the identification of the dominant environmental pressures affecting passerine communities over time are then related to the potential requirements for efficient bioindicators. Additionally, accuracy community model predictions is examined in relation to different trait groups to try to established how reliable their outputs may be for determining effective policy measures. Overall, climate variables were the key environmental drivers over the study period highlighting the importance of suitable conditions during the winter and early breeding periods. Also a shift in importance between pollution and land cover was observed through time with higher relevance of SO_4 concentration in the 1970s period and land cover on the 1990s which neatly correlated with reported changes in the environment on those particular variables. Hence, these results appear to once more indicate the suitability of passerines and their communities to monitor environmental change.

4.1 INTRODUCTION

Modern rates of anthropogenic environmental change are causing significant ecological consequences; therefore, a good understanding is needed about

how abiotic and biotic environmental factors interact with species dispersal processes and history across scales (Sala et al., 2000; Rojas-Ahumada et al., 2012; Wisz et al., 2013). To enable this understanding, scientifically-robust monitoring of the environment is needed to allow detection of both changes in the environment and on biodiversity (Morecroft et al., 2009). Developments in theory and statistical tests have led to a number of comparative studies looking into the influences of environmental and spatial factors on species distributions (Gilbert & Bennett, 2010; Mikuluyuk et al., 2011; Hajek et al., 2011; Rojas-Ahumada et al., 2012). For example, one outcome that has already received broad attention from the scientific community has been changes in species' geographic distributions with numerous studies confirming that range shifts are a widespread response to climate change (Walther et al, 2002; Parmesan and Yohe, 2003; Root et al., 2003; Parmesan, 2006).

A fundamental challenge in ecology is to understand the drivers of community composition, to help predict which species will occur together and where (Gilbert & Bennett, 2010; Wisz et al., 2013). The drivers that determined how communities were assembled during the past climate and environmental changes might be very different from what we are observing now (La Sorte & Jetz, 2010). Furthermore, depending on scale, the dominance of environmental pressures might change and even merge to create the species patterns currently being observed (Barbaro et al., 2007; Fig. 4.1). At coarser-scales, such as continental or regional extents (~200 to 10,000 km) geomorphological and bioclimatic processes can lead to environmental gradients, with animal distributions associated with climatic patterns or land cover types (Rojas-Ahumada et al, 2012; Barbaro et al., 2007; Kaboli et al 2006) (Fig 4.1). At coarse spatial scales (~200-10 km), micro-environmental, land-cover and other anthropogenic activities (e.g. pollution, fragmentation) are the most significant factors explaining species distribution patterns, biotic interactions factors such as predation/competition are mainly considered to become more significant at finer spatial scales (~ 1km) (Rojas-Ahumada et al, 2012; Barbaro et al., 2007; Kaboli et al, 2006) (Fig 4.1).

At the landscape level (~10km) , abiotic factors such as geology or microclimate interact strongly with biotic and human processes such as land use and disturbance regimes in complex spatial patterns of species occurrence that could be difficult to associate to single and simple explanatory factors (Barbaro et al., 2007; Fig. 4.1). However, this landscape level is the most relevant scale at which both conservation programmes and sustainable management practices are practiced (Barbaro et al., 2007; Wiens, 1994).

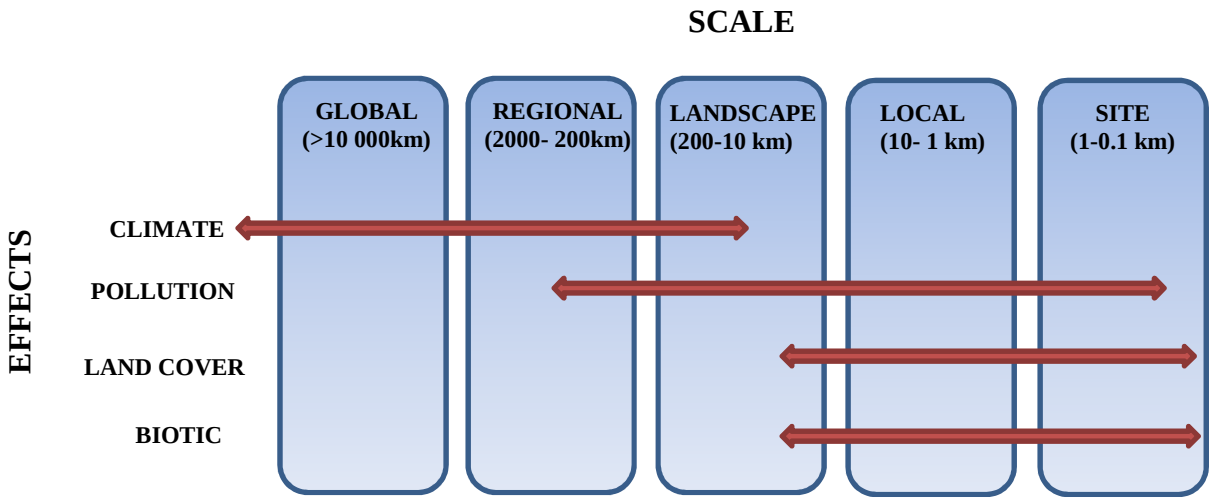


Figure 4.1. Spatial extents at which the influence of environmental factors is likely to be detected in spatially explicit data (adapted from Wisz et al., 2013).

As mentioned in Chapters 1 and 3, the most important direct drivers identified in the UK ecosystems according to the National Ecosystem Assessment, are: land use leading to habitat change, pollution and nutrient enrichment; overexploitation of terrestrial resources (harvest and resource consumption); climate variability and biological drivers such as invasive species (UKNAE, 2011).

With the observed patterns of biodiversity loss both at global, regional and national levels, there is an ever increasing need for reliable monitoring of

environmental change both at the physical and biological levels so that changed can be judge and appropriate conservation measures developed and monitored (Morecroft et al., 2009). With only a few studies integrating the different biotic, abiotic and spatial components potentially influencing species distributions, it would be of great value to develop further studies following this integrative approach to understanding the factors shaping species diversity and community composition (Yergeau et al., 2010).

As outlined in Chapter 3, multivariate and ordination methods are often used to investigate the associations between species occurrence or abundance and particular environmental variables of interest (ter Braak, 1986; Titeux et al., 2004; Peres-Neto & Legendre, 2009). Furthermore, and as outlined in the previous chapter, these approached allow for the integration of methods within the modelling framework that would take care of issues such as spatial autocorrelation or multicollinearity.

Both single species and community models are increasingly been relied upon to study the consequences of environmental and climatic change and to help develop adequate measures to protect vulnerable species (McPherson & Jetz, 2007). However, the reliability of models should be carefully assessed before their predictions are used to develop conservation measures. As McPherson and Jetz (2007) outlined, species traits can influence species distribution model reliability in two ways: a) by influencing the quality of the data available for the development of the model and b) certain characteristics may make it more difficult to statistically capture the relationship between the species' occurrence and the environmental conditions. For example species with broad ranges are less likely to be adequately captured by any one predictor, while migrants may be better captured by models based on coarse grained predictors (McPherson & Jetz, 2007).

The main objectives of this study were therefore twofold. First, I aimed to quantify the effects of the main environmental pressures (i.e. climate, pollution,

land cover and space) on passerine assemblages in the Britain and determine how these impacts may have changed between the two different atlas periods (1970 and 1990). A dominant role of climate and spatial factors was expected at this scale in both periods, however a decrease in pollution impacts was predicted in the second period (due to measures taken during the 70's to reduce emissions) and an increasing role of land cover and competitor species in the second period as impacts of agricultural intensification and fragmentation are likely to have increased in the past two or three decades.

The second objective was to identify which species were better characterized by these community models, in terms of their characteristic ecological traits, so that model accuracy and suitability could be taken into consideration when developing conservation measures/ actions plans based on these predictive models. In general it was expected that resident and spatially limited species would be better predicted compared to very specialized, migrant and common species.

4.2 METHODS

4.2.1.Study area and species data

Data on species presence and absence was obtained from the two breeding-bird atlases of Britain and Ireland. The first atlas used in this study collated data from the period 1968-72 (Sharrock 1976) and the second from 1988-91 (Gibbons et al., 1993). We refer to these two atlases/time periods as the 1970 and 1990 atlases respectively. For a full account of the methods see Gibbons et al. (1993). Both atlases documented the presence and absence of breeding bird species throughout Britain and Ireland within each 10x10 km square of their national grids. As land cover data was not available for Ireland, all Irish squares were excluded. Here for convenience the geographic study area is referred to as Britain and includes all islands where data were available. A total of 2358 grid square cells were used in the final analysis after accounting for differences

in the squares covered by the two time periods and the extent of the environmental data available Presence/absence data was available for 94 passerine species. Passerines were selected as the study group because of the ecological and behavioural diversity shown by members of this group and for their importance as bioindicators.

As a measure of competitive pressure, species from other groups which may have similar habitat requirements as passerines were identified (i.e. woodpeckers, pigeons, cuckoos). The number of competitor species per square grid was calculated for both time periods and included as one of the potential drivers of the passerine community.

Atlas data was also used to calculate one of the species traits used in the model accuracy analysis named, occupancy. This related to the ratio between the overall number of occupied squares over the two periods and the number of occupied squares in the second period.

4.2.2.Environmental predictors

For each 10 x 10 km square for each, data on a range of environmental predictors was collated and rescaled to the resolution of the species data (Table 3.1). Climatic data (i.e. temperature, precipitation and growing season length) were acquired from UKCIP (United Kingdom Climate Impacts Programme, http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/index.html) for 1960-1970 for the 1970 Atlas and 1980-1990 for the 1990 Atlas. Monthly average values of minimum, maximum and mean precipitation were calculated across the decade and then further averaged across seasonal periods considered to be important in avian life cycles (Table 4.1). Land cover data was extracted from the Ecochange project HISLU60 and PLCM1990 maps (1km^2 resolution). Further details on the development of these land-cover maps and the modelling process are provided by Hazeu et al.(2008). These data represent the mean cover (area) of the respective class in each 10km grid cell.

Air pollution concentrations were obtained from the FRAME project and they represent air concentrations of the main pollutant compounds for 1990 and 1970 (Malgorzata et al. 2009).

To minimize the effect of multicolinearity among environmental predictors (particularly within the climatic factors) and to avoid overfitting, the variance inflation factors (VIFs) and correlation values between variables (particularly among climatic variables) were explored and those predictors with high values ($r>0.8$ and $VIF>10$) were excluded from the analysis.

Table 4.1. Environmental predictor variables calculated for each period in the analysis of drivers if passerine community composition.

Variable set (number of variables)	Predictors	Details of predictors
Climate (11)	Temperature min.	Early breeding (Mar-May), Total breeding period (Mar-Aug), Nestling period (May-Aug), February(~pre-breeding conditions), October(~post-breeding conditions)
	Temperature max.	Late breeding (Jun-Aug), Early breeding (Mar-May, Nestling period (May-Aug)
	Precipitation	Early breeding (Mar-May), Total breeding period (Mar-Aug), Nestling period (May-Aug)
Land use (7)	HISLU60 and PLCM1990 maps from Ecochange project	Mean cover of: urban, arable land, grassland, forest, non-agricultural land, inland water and sea.
Pollution (7)	Air pollutant concentrations from FRAMe project	NO3 , HNO3, NH4, SO4 , SO2, NOx, NH3

4.2.3.Spatial predictors

To account for spatial structure in the data, a set of spatial predictors were calculated using Principal Co-ordinate Analysis of Neighbour Matrices (PCNM) analysis as described in Chapter 3 (Borcard & Legendre, 2002).

This analysis yielded 1204 PCNM eigenvectors (~ 2n/3 where n is 2358 sites) with positive eigenvalues, reflecting positive spatial autocorrelation, for use as spatial predictors in multivariate analysis. The analysis was further restricted to those PCNM eigenvectors that represented statistically-significant spatial autocorrelation according to Moran's I (p-value <0.05) and were significant taking into consideration *a priori* biological knowledge (Blanchet et al., 2008).

4.2.4.Statistical analysis

The avian assemblages for the two time periods were related to environmental and space variables using CANOCO 4.5 software (ter Braak & Smilauer, 2002) and the vegan package (Oksanen et al. 2010) in the R statistical environment (R, 2008). Initial inspection of the avian dataset using Detrended Correspondence Analysis (DCA, ter Braak & Smilauer, 2002) produced eigenvalues of 0.242, 0.088, 0.052, and 0.034 and gradient lengths of 3.396, 4.201, 3.51, and 1.935 for the first four axes respectively. Since, the majority of gradient lengths were greater than 3 and considering the scale of the study, unimodal ordination methods were deemed appropriate for this study; here Canonical Correspondence Analysis (CCA) was used (ter Braak & Smilauer, 2002). CCA is an eigenvector ordination technique for multivariate direct gradient analysis and constitutes an extension of multiple regression analysis for multivariate responses (Palmer, 1993).

Forward selection was run within each time period to optimize the fit of the model and identify those variables that explained most of the observed variance in the data. Forward selection was carried out with Monte Carlo permutation tests (999 permutations; p<0.05) in CANOCO to retain only the most important variables and avoid the increase of explained variation by chance alone. The selection procedure is not species-specific; variables are picked in order of decreasing proportion of variation explained in the species dataset as a whole (Guisan et al. 1999). To prevent over-estimation of variance explained by a given predictor set two stopping criteria were used: an alpha significance level of 0.05 with p-values (*P*), obtained from permutation tests (n=9999), corrected

after Sidak (1967) for the number of tests, where $P_s = 1-(1-P)^k$ where k was equivalent to the number of variables in the predictor set, (ii) the adjusted coefficient of multiple determination (R^2_a) of the global model with all explanatory variables (Blanchet et al., 2008). Only predictors with a significant p-value after Sidak correction and a positive R^2_a were retained for further analysis.

This process was run with raw data and also with detrended data (after Borcard et al. 2004). Detrending was used to remove the strong north-south gradient observed in the environmental data sets which may have obscured the effects of the different environmental and spatial factors; here only the detrended results are discussed.

The relative role of climate, land cover, pollution and space variables in driving bird communities was evaluated using variance partitioning where the total percentage of variation explained by a Canonical Correspondence Analysis (CCA; Legendre & Legendre, 1998) was partitioned into unique and shared contributions of the sets of predictors (Borcard, 1992). Analogous to multiple regression, the amount of explained variance in CCA or redundancy analysis is influenced by the number of explanatory variables as well as the sample size (both number of sample sites and species in this examples) (Peres-Neto, 2006). Thus, the unadjusted and adjusted coefficients of determination are reported for each fraction of the variation in communities. Significance of fractions was tested by permutation tests using 999 randomizations (Borcard, 1992).

To quantify the accuracy of community models to explain the variation observed in each species distribution pattern in relation to characteristic species trait, GLM models with % of variance explained and species traits with stepwise selection was used as described in the previous chapter. The traits used in this analysis were related to life history, ecological and phenological characteristics of the bird species under study which are thought to play a significant role in their distribution (Table 4.2).

Table 4.2. Description of species-specific traits used in the analysis

Variable	*Description*
Migration strategy	Nominal variable: Resident (1), partial migrant (2) and migrant (3)
Diet type general	Nominal variable: seed eaters (0), insectivorous (1) , generalist (2)
Habitat preference	Nominal variable: Farmland specialist (1), woodland specialist (2), generalist (3), water related (4), urban and others (5).
Av. body weight	Average body weight for the species (♀♂)(g)

4.1 RESULTS

The CCA analyses produced eigenvalues of 0.092 and 0.035 for the first two axes in the first atlas period (total inertia in the model 0.216) and 0.1 and 0.049 for the second atlas period (total inertia in the model 0.245); the models explained 58.7 % and 60.7% of the variation for the two periods respectively.

The distribution of the passerine communities showed considerable similarities in both time periods with Axis 1 being correlated with February minimum temperatures (Fig 4.2 and Fig 4.3). Axis 2 is largely correlated with early spring precipitation (+ve), agriculture (1990 only, +ve) and pollution impacts (-ve, SO_4) and maximum autumn temperatures (-ve).

In both time periods the February minimum temperature explained the greatest proportion of variation in the community (3.9–3.5 % respectively, Table 4.3). This was followed by pollution (i.e. SO_4) and late breeding maximum temperature in the 1970 period (1.8% and 1.3% respectively, Table 4.3a) and early breeding precipitation and competitor number in the 1990 period (1.8-1.5 % respectively, Table 4.3 b). Space explained a significant proportion of the variation in both years (mainly PCNM1), and these spatial vectors represent broad-scale spatial gradients across Britain (Fig 4.4).

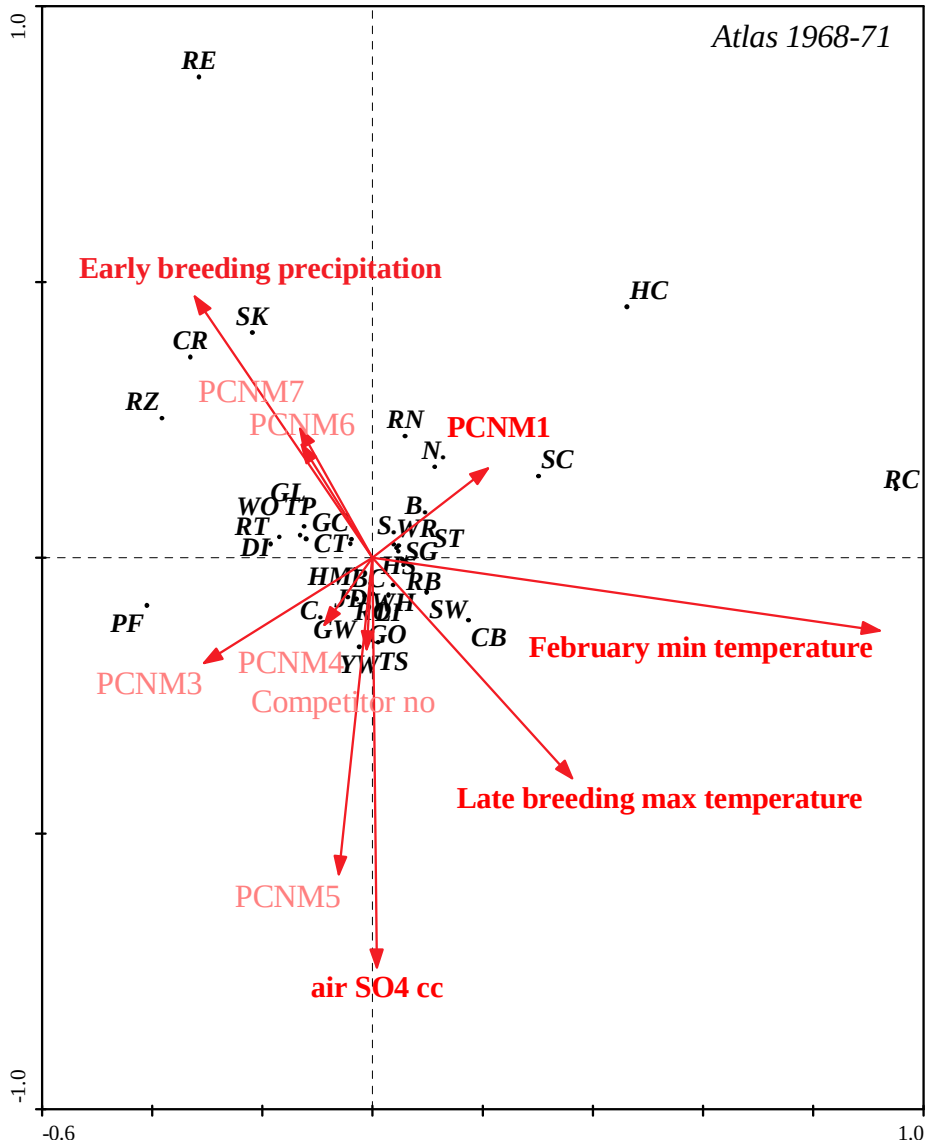


Figure 4.2 CCA biplot of the first and second axes of British Passerine communities derived from the 1970 Atlas. The five most significant variables are in bold and they relate to space, climate and pollution variables. Environmental variables have been detrended; species codes in Appendix, supplement B.

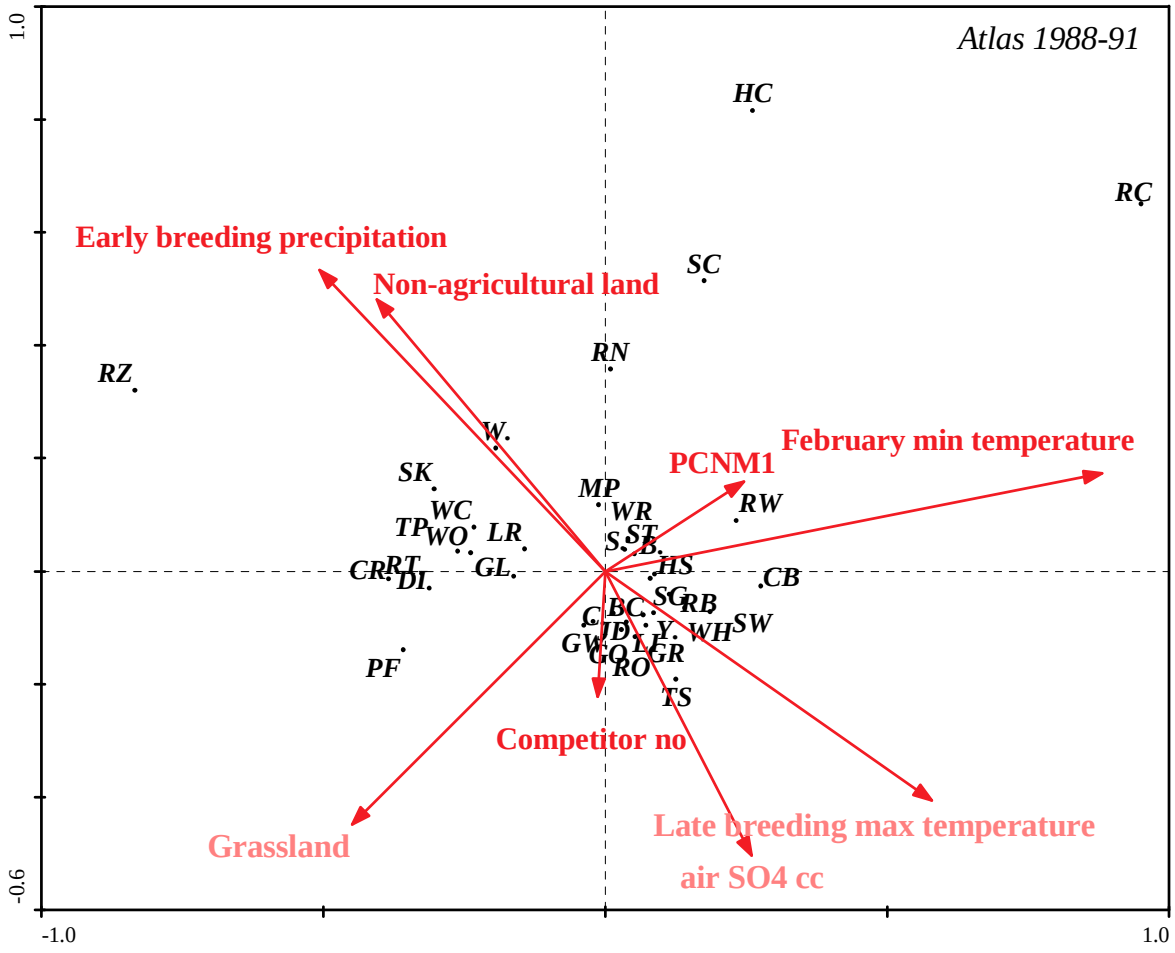


Figure 4.3 CCA biplot of the first and second axes of British Passerine communities derived from the 1990 Atlas. The five most significant variables are in bold and they relate to space, climate and land cover variables. Environmental variables have been detrended; species codes in Appendix, supplement B.

In addition to the drivers mentioned above, in the second period land cover also had a significant effect albeit a small one (i.e. area of non-agricultural land: 1.2%, grassland area: 0.5 %). Though competitor numbers has one of the smallest contributions during the first period it increases notably in importance during the second period (from 0.5% to 1.5%).

After identifying the main variables explaining the observed variation in community composition, they were grouped into different environmental sets to investigate the importance of different factors in driving species assemblages (Table 4.4). In the case of the 1990 period climate, pollution and land cover variables were pooled together in the abiotic factor group, whereas in the 1970 model only pollution and climatic factors constituted the abiotic cluster. These data were used in subsequent variation partitioning.

Table 4.3. Detrended environmental variables and spatial vectors selected by forward selection procedure in order of inclusion in the final model. The percentage of the total variance explained by the variable in their model, R^2_a and sidak corrected p-value are reported. The selection criteria consisted was based on R^2a >0 and Sidak corrected p-values all variables presented were < 0.02. a) 1970 atlas, b) 1990 atlas.

a)

Variable	% total inertia	R^2_a
February min temp	3.932	0.039
SO_4	1.835	0.018
Late breeding max temp	1.311	0.012
PCNM 1	1.180	0.010
Early breeding precp	0.786	0.006
PCNM 3	0.786	0.005
Competitor no	0.524	0.002
PCNM 5	0.524	0.002
PCNM 6	0.524	0.001
PCNM 7	0.524	0.001
PCNM 4	0.524	0.001

b)

Variable	% total inertia	R^2_a
February min temp	3.514	0.035
Early breeding precp	1.807	0.017
Competitor no	1.506	0.014
No. agricultural land	1.205	0.010
PCNM 1	1.004	0.008
Late breeding max temp	0.803	0.006
SO_4	0.703	0.004
Grassland	0.502	0.002

Table 4.4 Predictors included in the variance partition analysis after forward selection of detrended data.

Environmental variable set	Sub-set	1970	1990
Abiotic	**Climatic**	February min temp, Late breeding max temp, Early breeding precip	February min temp, Late breeding max temp, Early breeding precip
	Pollution	SO_4	SO_4
	Land cover	-	Non- agricultural land, Grassland
Biotic		Competitor no	Competitor no
Spatial		PCNMs: 1, 3, 4, 5, 6, 7	PCNMs: 1

Figure 4.4. Spatial predictors that explained a significant amount of variation in the avian bird communities in 1970 (all) and 1990 (PCNM 1 only). These PCNM vectors describe variable degrees of possible spatial structure with lower vectors representing regional-scale groupings and higher order vectors representing more local-scale groupings. Colour represents the sign (- white, + black).

4.1.1.Identification or the most important environmental of drivers of avian community composition in Britain in the two study periods

The independent effects of the different environmental sets are outlined in Table 4.5. Climatic variables had the greatest largest significant independent effects in both periods (5.9% in 1970 and 4.1% in 1990) and pollution accounted for 1.4% of the variation in 1970 reducing to 0.7% by 1990. Land-use variables were not significant in 1970 but by 1990 the impacts of the cover of grassland and non-agricultural land were considerable. The effect of biotic factors (competitor species) increased by almost 4 fold between the two periods (from 0.5 to 1.7%) whereas the effects of spatial variables have declined (3.7% to 1%). The overall amounts of variation explained are relatively low but they are all significant and they represent 32.4% and 39.1 % of the equivalent unconstrained correspondence analysis (1970: R^2 first 11 axes of CA=38.3, R^2_a=38, 1990: R^2 first 8 axes of CA=28.3, R^2_a=28).

4.1.2.Performance of the different community models in relation to species traits for the two study periods

On average, the amount of variance explained for individual species by the community models was 17.3±11.4% for the first period and 12±4.6% for the second. For the 1970 period the lesser whitethroat produced the best-fit model with 43.3% for the variation explained and the tree creeper had the poorest with only 1.6% of variation explained. In the second period, 1990, the best explained species was the tree pipit with 20.7% and the worst species still corresponded to the spotted flycatcher average with 3%.

The final model relating the amount of variance explained by the community model (i.e. with all environmental and spatial factors) to species traits was only better than the saturated and null models in the first time period, with a 46% adjusted D^2 (Table 4.6a). In relation to species traits, only prevalence was significant, with more accurate models for less prevalent species (Table 4.6 b). When the relationship between prevalence and the other characteristics was explored, it showed a relationship between average body weight, migratory

behaviour and habitat generalism with prevalence decreasing with larger body weights, long distance migration and farmland and urban specialization (Table 4.7).

Table 4.5 Independent effects of selected drivers of passerine community in the UK derived from variation partitioning; the % inertia accounted for is presented along with Sidak's adjusted p-value and the adjusted R^2.

Environmental variable set	Sub-set	Details	1970			1990		
			Total inertia (%)	R^2_a	Sidak p-value	Total inertia (%)	R^2_a	Sidak p-value
Abiotic	Climate	Late breeding max temp, February min temp, Early breeding precip	5.91	0.06	0.003	4.09	0.04	0.003
	Pollution	Air cc. SO_4	1.40	0.01	0.001	0.66	0.01	0.001
	Land cover	1990: Grassland, no agricultural land	-	-	-	1.52	0.02	0.002
Biotic		Number of competitor species	0.48	0.005	0.001	1.66	0.02	0.001
Space		1970: 1,3,4,5,6,7 1990: 1	3.69	0.037	0.006	1.01	0.01	0.001

Table 4.6. Models for variance explained and characteristic traits of the studied species. a) Model performance for global, null and final models for variance explained for each species by the community model based on Adj D^2 and AIC_c for the two time periods, b) predictor direction in the final models for the two time periods.

a)

	1970		1990	
	AIC_c	$Dadj^2$	AIC_c	$Dadj^2$
Saturated model	374.6	0.44	323.5	0.25
Final model	358	0.46	297.4	0
Null model	388.2	0	297.4	0

b)

Species traits	1970			1990		
	Estimate	SD	p-value	Estimate	SD	p-value
Final model (var expl~Occupancy)	-34.34	5.2	<0.001	-	-	-

Table 4.7. Trait coefficients for the model relating species occupancy and other species characteristic traits.

Species traits	Prevalence model		
	Estimate	SD	p-value
Log(Average body weight)	-0.04	0.03	0.15
Migratory behaviour-partial migrant	0.014	0.08	0.85
Migratory behaviour-migrant	-0.127	0.07	0.07
Habitat-woodland specialist	-0.074	0.09	0.44
Habitat-generalist specialist	0.052	0.08	0.52
Habitat-water related	-0.231	0.11	0.04
Habitat-urban/other	0.033	0.13	0.80

4.2. DISCUSSION

4.2.1.Drivers of passerine community in the UK

As expected at this landscape scale (i.e. 10 km) the main drivers of community composition are abiotic factors and particularly temperature and precipitation, though there is also a considerable effect of pollution and land cover, with the impacts of pollution being strongest in the first period and that of land cover in the second.

Within the two main climatic factors selected, there appears to be an overriding importance of winter temperatures in both time periods. Mortality in birds has been reported to occur in response to prolonged periods of continued adverse conditions particularly in winter (Robinson et al., 2007). Winter is clearly a key period in a bird's life cycle, with conditions being adverse and food supplies limiting, hence if due to climatic change these conditions become more favourable (i.e. increasing temperatures leading to more foraging opportunities), survival and increases in populations are also likely to occur (Crick 2004; Julliard et al. 2004; Robinson et al., 2007). Furthermore, it has been shown that winter temperatures are associated with northern range limits of species (Root, 1988), hence change in these could trigger range/distribution changes in species as reported in previous studies (Parmesan, 2006; Walther et al., 2002).

The extensive intensification of industrialization and energy production during the 1950-70s resulted in increased burning of fossil fuels, causing increased emissions of acidifying pollutant (i.e. sulphur (S) and nitrogen (N) compounds) into the atmosphere (Vuorenmaa, 2004). Total European S emissions exhibited a sharp increase during the 1950s and 1960s, peaking in the mid-1970s (Fowler et al., 2005; Vourenmaa, 2004). During these decades significant effects of deposited sulphur were detected such as reduced crop growth and elevated acidity in water (RoTAP, 2007). Also eggshell thinning and reduced egg mass was reported for bird populations residing in these polluted areas as well as changes in energy expenditure with greater proportion of the day being spend foraging and less time resting or available for self-maintenance, predator avoidance or breeding (O'Halloran et al., 1990; Ormerod et al., 1988). During the 1980s, emissions of SO_2 started to decrease slightly and due to successful implementation of emission reduction agreements (i.e. the Convention on Long-Range Transboundary Air Pollution (CLRTAP), Gothenburg protocol) with the total emission reduction of SO_2 between 1980 and 2000 adding up to 60% (Vourenmaa, 2004). As the concentrations of these pollutants declined so it seems that did the relevance of this factor in determining the composition and distribution of bird communities in the study area.

On the other hand, land use change has increased in importance as a driver of passerine community composition. During the first period, no land cover variables were selected as main drivers of bird communities while on the second period they became highly important. Again, this could be due to the observed changes in agricultural management. . As outlined in the introduction, during the 1940-1970 there was an increased mechanization and intensification of farmland in the UK with amalgamation of fields into larger units and the consequential loss of the hedge-ditch-verge complex that provided valuable habitat heterogeneity in many rural landscapes (Jarvis, 1993). According to Jarvis (1993) between 1945 -1970 there was an average 500 km of hedgerows removed from England and Wales. Hedgerows are prime breeding habitat for a

number of farmland species such as yellow hammer (*Emberiza citronella*) or whitethroat (*Sylvia communis*) as well as providing food, shelter and nesting sites for a larger range of species (Osborne, 1984). Chamberlain et al. (2000) also examined changes in agriculture in terms of crops areas, livestock numbers, grass production and pesticide use in Egland and wales during a period similar to this study (1962-1995). According to their study, the period of 1970-1988 saw the most agricultural intensification and it was characterized by increases in the area of autumn-sown cereals and the use of pesticides and inorganic fertilizers. Furthermore, they reported a correlation between the change in agricultural management and bird population declines with a time lag in bird response. Hence, the change in importance of this land cover use observed in this study could also be an indication of the response of bird populations to the increased intensity of agricultural areas. Highly mechanized farms have been shown to affect birds by increasing brood and nest losses in ground nesting species as well as reducing grain wastage (available food for granivorous birds) and compressing the period in the farming year where food in available for species (Jarvis, 1993).

In fact, the observed increase in importance of non-agricultural and grassland areas in the second period could be an indication of more birds moving into non-agricultural land and away from the intensely used farmland areas as a consequence effects improved habitat features such as stubble or wild bird cover (Reynolds et al., 1994; Branbury et al., 2004). The practice of leaving arable land uncroppped for a period of time as bare fallow declined markedly during the post war period, but the introduction of set-aside police since the late 1980s has taken large areas out of production which could also be related to the increased in importance observed in the second period of our study.

In terms of competition, though a small effect was detected in either period, it doubled in importance as a driver of community composition from 1970 to 1990. After looking at number of species per square in both passerine and competitor species, both groups appear to be simultaneously increasing over the study

period. This seems to indicate some sort of heterospecific attraction or perhaps a common response of both species. The idea of heterospecific attraction is based on the concept that conspecifics attract other individuals to settle down in adjacent territories and form aggregated distribution patterns (Monkkonen et al., 1990). This aggregated distribution can develop as a mechanism that: a) provides protection against predators by means of cooperative defence or information delivery or b) benefits individuals if settled neighbours reflect the quality of the habitat (Monkkonen et al, 1990). The fact that this phenomenon is more prevalent in the second period could also be indicative of the impacts of the agri-scheme in producing a larger range of suitable habitat that a range of species could use in a variety of ways.

Finally, though climate was expected and proved to be the prime driver of community patterns at this scale, significant impacts of other drivers were also detected at this scale, most significantly land use, pollution but also a minor effect of competition. Even though traditionally they might be thought of as more local scale factors and population level drivers their signs were still apparent at this scale. This emphasises the multi-scale operation of these pressures and the importance of studies and analysis where all potential drivers are taken account simultaneously.

The observed effect of climate has already been reported as a key factor in driving communities at this scale in a variety of previous studies. However the interesting outcome of this study is the detectable signal of land cover and competition which have been assumed to be trivial at this geographical extent. This study shows that despite the tremendous importance of climate at this larger scale the effects of other factor are still relevant and highlights the interacting effects that all environmental factors have on species distributions. Other studies looking at the roles of climate and land use in driving biodiversity patterns at large scale have also identified similar patterns to the ones outlined in this study (Schrang et al., 2009; Kosicki & Chylarecki, 2012). For example Schrang et al., (2009) showed that bird species richness follow a gradient of

temperature and precipitation across the region and that species show differential responses to different land covers (i.e. positive associations with native vegetation cover and negative ones with agricultural use).

4.2.2.Relationship between ecological traits and community model accuracy – for which groups of species are community models likely to give good predictions of distribution and distribution change?

In terms of model accuracy, the final models do not seem to be very precise at describing species distribution in the overall community for either period though the accuracy levels are consistent with other community modelling studies (Titeux et al. 2004). As previous studies indicate, the best scale for modelling species distribution varies with species ecological characteristics and the interaction between model accuracy and ecological traits might vary with the spatial resolution of the analysis (McPherson & Jetz, 2007). Though as presented in the previous section, our study detects the effects and impacts of all variables under study even at this coarse landscape scale, in order to improve the predictions of the final model, a resolution closer to the species habitat perception, such as local or site level, may be more suitable (i.e. 5-1 km).

Nevertheless, a signal related to species occupancy was detected in relation to model accuracy indicating that species with lower occupancy level were better modelled by these community models. This pattern of model accuracy has been reported in other studies where species with larger ranges appeared to be more difficult to model (Stockwell & Peterson, 2002; Segurado and Araujo, 2004). However, this is still a contentious issue with studies also supporting the opposite pattern, of species with larger ranges yielding better models (Garrison and Lupo, 2002).

Also the present study revealed that species occupancy is related to other species traits, namely average body weight, migration behaviour and habitat

preference. The patterns observed here (i.e. lower occupancy in large bodied species, migrants and specialized species) have been observed in other studies. A negative correlation between geographical range and body mass was reported by Gregory (1995) in his analysis of British birds. In this study, though body weight appears related to occupancy, and therefore indirectly to model accuracy, its effects are so minimal that inferences cannot be made about its contribution to model accuracy.

In terms of migratory behaviour, it appears to be significantly related to species occupancy. Just by means of the behavioural constraints that migration imposes, migrant species may be more variable in time and space as their occurrence patterns will be determined by seasonal conditions rather than conditions throughout the year (MacPherson & Jetz, 2007). Hence their occurrence and occupancy patterns in a particular environment will not be as constant as in the case of either residents or even partial migrants, as observed in this case, making model predictions for these species that much harder and hence reducing model accuracy. In terms of habitat use, other studies have revealed that increasing habitat tolerance affected model accuracy unfavourably (Segurado & Araujo, 2004; Brotons et al., 2004; MacPherson & Jetz, 2007). In this study, though habitat use seems related to species occupancy levels, the different categories of this trait appear insignificant (except in the case of wetland specialist species) therefore no substantial assumption in its effect on model accuracy can be made.

As indicated by the results of this study passerines appear to be good indicators of environmental change even at coarse scales. Signals of all potential drivers have been detected and correspond to reported changes in these factors over the timescale of the study. Furthermore, the fact that changes also appear to correspond to the implementation of particular conservation actions and policy plans seems to indicate that they could be used in community models as potential tools for monitoring management outcomes. However, as shown by the model accuracy analysis these community models will not be appropriate for

all species as particularly traits (i.e. occupancy and migrant behaviour) will affect their applicability. Also it would be of great importance to develop these models at the adequate scale in order to maximize their accuracy and therefore their suitability as monitoring and policy guidance tools.

Chapter 5 : Niche dynamics of passerine birds in Britain, a coarse-scale method

ABSTRACT

The niche is a concept that describes the ecological space occupied by a species. The extent to which niche space, either realised or potential, is responsive to environmental change is relatively unknown. This chapter explores niche dynamics in UK passerines over time and demonstrates that the realised niche space is not a static concept and actually can and does change over time. The extent to which niche parameters vary between species is studied in relation to species biology to determine if particular sets of traits have a bearing on the resilience of these niche parameters under study. Specialist species and species with more inflexible life history and phenology were more likely to show changes in relative niche measures than more flexible species.

5.1 INTRODUCTION

The species niche is a key concept in ecology. Nearly a century ago, Grinnell presented the concept of ecological niche asa set of environmental conditions that restrict each species, through “physiological and psychological respects” to a geographical range where it can prosper (Grinnel 1917). Grinnell (1917) discussed the important role played by temperature in ultimately defining range boundaries, but noted that within the limits of physiological tolerance, numerous other factors, including inter-specific competition, can determine realized range boundaries (Tingley et al., 2009). Later, Hutchinson (1957) also proposed the concept of species fundamental niche as “volume in which every point…corresponds to a state of the environment that would permit the species…to exist indefinitely”.

The general notion that environmental limiting factors define the niche where a species can have a positive growth still remains the dominant explanation for range boundaries, suggesting that the spatial extent of the range for most species approximately equals to the geographical expression of a species' niche (Tingley et al., 2009). Therefore, we can differentiate the two concepts of niche, the fundamental (i.e. potential environmental conditions available for the species) and the realized (i.e. current environmental space occupied by the species) (Fig 5.1).

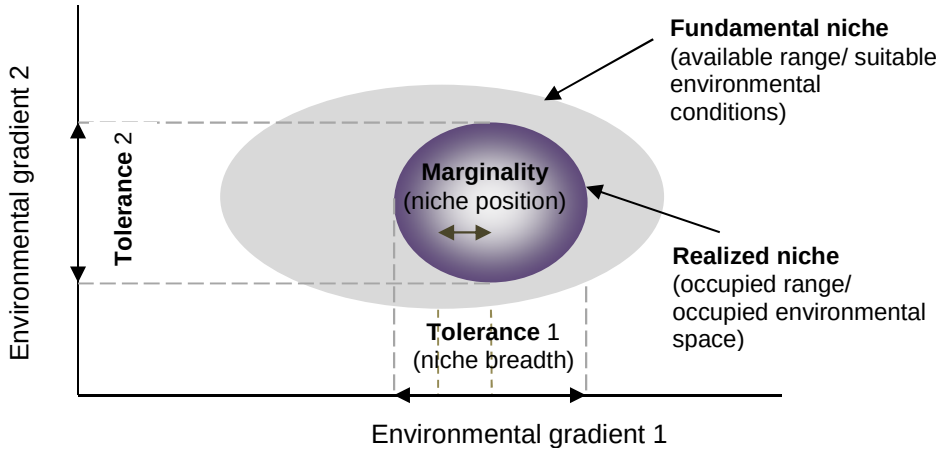


Figure 5.1. Fundamental and realized niche concepts and main niche parameters (i.e. marginality and tolerance). The marginality of a species relates to its niche position or the average conditions it occupies across the potential available. Tolerance on the other hand represents the range of resources use by the species.

Assessing differences in either fundamental or realized environmental niche of a species requires identification and consideration of the factors that influence its distribution (Broennimann et al., 2011). The environmental conditions comprising the realized niche can be described using a set of geographically-referenced environmental variables (Broennimann et al., 2011). Furthermore, temporal sampling of changing environments makes it possible to measure the

dynamic relationship between the environment, a species' climatic requirements and its realized range (Tingley et al., 2009).

In recent decades there have been significant developments in the area of ecological niche models (Holt, 2009). These are statistical models that relate spatially-explicit information about species geographical distributions and collections of environmental variables using different algorithms and methods to generate a species distributional or predictive habitat model that represents a species' realized niche, as expressed in its habitat breadth or geographical range (Holt, 2009). Statistical niche models, therefore, potentially provide useful tools for identifying examples of niche conservatism and quantifying niche evolution at the species and higher levels (Holt, 2009). For example, at the species level, one could look at the variation in niche parameters along some niche dimensions to establish which changes in conditions are driving niche evolution and quantify if different factors explain the observed differences (Holt, 2009). Also a species' ability to persist in the face of environmental change could be investigated by looking at the contribution of niche evolution to species persistence and how this niche evolution change over time is influenced by species plasticity. Moving to a community scale, for a given environmental change some species in a community will show niche evolution whereas others will display niche conservatism, so one could look at what accounts for such interspecific variation (Holt, 2009). Though it has been recognized that a variety of ecological parameters are flexible, no comparative study per se has looked at the variation in niche parameters and traits within a clade (Losos, 2008). In general species with broader ecological resource use characteristics (i.e. wider habitat or diet range) and more flexible phenological traits (i.e. extended laying periods or earlier laying dates) may be better suited to deal with environmental changes and will have broader environmental niches and may not present much niche variation over time (i.e. large tolerance and minimum marginality). Species with more restricted ecological characteristics (i.e. either diet or habitat specialists) or with less phenological flexibility (i.e. set laying dates or restricted laying periods) may be more prone to negative effects when faced with changes

in their environment (i.e. small tolerance and large marginality). The latter species may be more likely to have rapidly shifted range to track the suitable environmental conditions and present larger changes in terms of their niche parameters (i.e. marginality and tolerance) as they try to adapt to the changing environmental conditions.

Methods for quantifying species niche and estimating niche differences typically rely on either ordination techniques (Thuiller et al., 2005) or species distribution models (SDMs; Guisan and Thuiller, 2005). Ordination techniques allow for direct comparisons of species-environment relationships in environmental space, and employ various maximization criteria to construct synthetic axes from associated environmental variables (Broennimann et al., 2011). In contrast, SDMs involves calibration (for each species) of statistical or machine-learning functions that relate environmental variables to geo-referenced data on species occurrence.

A species' niche can be described through its position and breadth along well-defined gradients of resources or environmental conditions (Barnagaud *et al.*, 2012). A species' niche position usually reflects the average level of a resource that it exploits (or the average conditions it copes with) across its distribution. It can, therefore be regarded as a coarse-grained measure of resource use (Barnagaud *et al.*, 2012). On the other hand, niche breath (or specialization) corresponds to the range of the resource used by the species (i.e. the deviation from its position that it tolerates). Hence, niche position and niche breadth provide complementary insights into the influence of environmental gradients on species or communities (Barnagaud *et al.*, 2012).

The position of a species depends on its deviation from the distribution of a hypothetical species that tolerates "average" habitat conditions and is uniformly distributed across all habitat conditions (i.e. species using the fundamental niche; Heino, 2005). This deviation has been termed species marginality, and measures the niche position of species; species with high values have marginal

niches and those with low values having non-marginal niches (Heino, 2005) (Fig 5.1). An additional variance term that measures niche breadth is tolerance; this measures the amplitude in the distribution of each species along the sampled environmental gradients (Fig 5.1).

Niches can, however, evolve (Holt, 2009). If ranges are moulded by physiological limitations that remain fixed over the time scale of comparison, then species should also move across the landscape as averages and extremes of temperature, precipitation and other extrinsic factors change over short time spans (Tingley et al., 2009). This process, by which species follow limiting environmental boundaries through geographical space to remain in a favourable climatic space, is called niche tracking (Tingley et al., 2009) (Fig 5.2b). Parmesan and Yohe (2003) carried out a global meta-analysis and reported that 81% of the species studied shifted ranges in response to recent climate change, indicating a tendency for niche tracking. However, 19% of the studied species either moved in directions opposite than predicted or presented no change in their ranges, which could indicate heterogeneous species responses in terms of niche dynamics (Parmesan & Yohe, 2003).

The term “niche conservatism” could be used when a species’ niche is constant across its range or evolutionary history (Wiens & Graham, 2005; Holt, 2009). It has recently been looked at in different theoretical and practical studies (Bridle and Vines, 2006; Wellenreuther et al., 2012) (Fig 5.2a). Whether niche evolution or conservatism is observed will depend both on factors intrinsic to a species (i.e. characteristic traits, genetic variation, etc.) and extrinsic factors (i.e. spatio-temporal structure of the environment, including other species).

Changes in site occupancy driven by changing environmental conditions are manifested as range shifts (Tingley et al., 2009) (Fig 5.2b). Range change, and thus the ability of species to track their climatic niche, occurs at two primary scales (Tingley et al., 2009). At the scale of the site where the individuals live, niche tracking during environmental change can lead to three outcomes: i) the

site may remain within the climatic niche of the species despite climatic change, allowing individuals to continue occupying it (Fig 5.2b1), ii) the local environment may shift outside of the climatic niche, leading to extinction at the site through reduced survival or reproductive success or emigration (Fig 5.2b2.1), iii) the local environment may shift inside the climatic niche allowing colonization if dispersal occurs (Tingley et al., 2009) (Fig 5.2.). Depending on the time scale, the magnitude of environmental change, the size of the niche, the rigidity of the niche boundaries, and other natural characteristics of the organism, any or all the outcomes may be expected results from of climate change at the site level (Tingley et al., 2009).

Empirical data can be used to explore whether changes in niche parameters are related to environmental pressures, as for example, climatic changes (Tingley et al., 2009). Given that the climate has generally become warmer and drier in most temperate regions during the past decades, a species showing niche conservatism would exhibit movement of its climatic niche toward a warmer drier environment. If species do present niche evolution and climatic conditions shift away from the average niche conditions, more vagile species might adjust their occupancy by colonizing newly favourable sites or abandoning unfavourable sites, which will result in an occupied range that tracks the climatic niche, while more adaptable species might just present no significant range movements despite the observed environmental change.

Understanding niche dynamics would be a prerequisite to be able to predict patterns of biodiversity in future climates or in areas distinct from where models are fitted (Pearman et al., 2007).

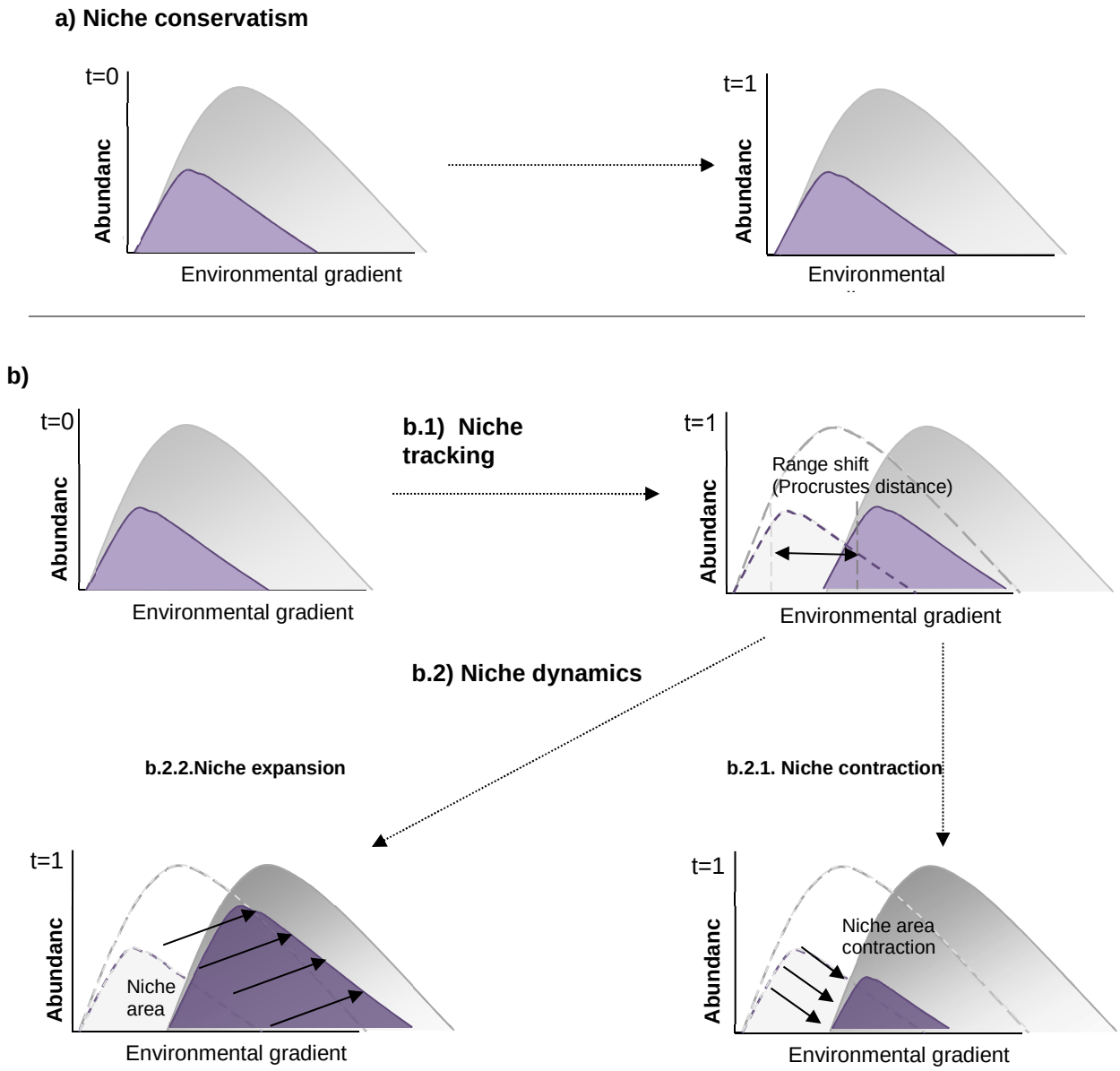


Figure 5.2. Different niche dynamics scenarios. There are two snapshots of a species niche in time with three different outcomes (the black arrows indicate the evolution of the species niche through time): a) both the available environmental conditions and the species niche remain constant over time (niche conservatism); b) environmental conditions change between the two time periods and the species react to these changes. In the first scenario, the species are able to adapt and track the changes in order to maintain their optimum conditions (i.e. niche tracking, b.1). If environmental change occurs and species are force to a new environment where conditions are not optimum, a niche contraction is observed as suitable conditions available for the species are reduced (b.2.1.) .On the other hand, if species move to areas where new conditions are optimal and allow them to proliferation and colonize new areas a niche expansion is detected (b.2.2.).

The impacts of environmental changes depend not only on the nature of the environmental factor(s) concern but also on certain properties of the species, its population, or community (Jarvis, 1993). How a species react to environmental changes depends on their resilience (the extent to which they can tolerate or accommodate stress/ disturbance) or ecological resilience (the extent to which a population or community can return to their original state after being disturbed) (Jarvis, 1993). Hence appropriate ecological metrics are required to not only measure these impacts but also influence policy and management action (Everard, 2008).

As mentioned in Chapter 1, the suitability of birds as environmental indicators is already recognized and applied in the UK, Europe and the USA (Environmental Protection Agency, 2006; Everard, 2008). This is because birds are widely-distributed, they are conspicuous and recognized by the public, they are mobile and respond rapidly to change, and they also depend upon a matrix of habitats across landscapes (Everard, 2008). Data are recorded widely throughout the UK and Europe, from which population trends may be deduced with reasonable temporal resolution (Gregory et al., 2005). Bird population data are analysed not only for the UK Government as sustainable indicators (DETR, 1999), at country, UK and regional scales, but also at the European scale (PECBM, 2006) providing further context for interpretation of local trends (Everard, 2008). Birds are therefore perceived as good indicators of the broad state of biodiversity because they occupy a wide range of habitats, they tend to be near the top of the food chain and they are supported by considerable long-term data. Moreover, as they respond quickly to environmental pressures and depend upon different food sources and habitats means that the act as effective surrogates for impacts of a wide range of environmental changes (Everard, 2008).

As mentioned before, in terms of niche dynamics, for a given environmental change, species can differ greatly in their tendency for niche evolution (Holt, 2009). While some species in a local community exposed to that change may

show niche evolution, others may display niche conservatism or contraction, leading to population extinction/decline. So what accounts for such inter-specific differences? And how can this help the development of more efficient bio-indicators and our overall understanding of rarity? For example, Bradshaw (1991) showed that some plant species showed significant niche expansion via the development of tolerance to toxic soils, while other species in the same communities did not.

Here I use a unique dataset of bird distributional data (i.e. two consecutive breeding bird atlas) over a 20 year period to test the degree to which 50 passerine bird species distributed across the British territory track a three-variable environmental niche (i.e. climate, pollution ad space) through space and time. I expect species to have responded to climate and environmental change by either modifying their ranges to remain within their original climatic niche and/or otherwise change in their characteristic niche parameters (position and breadth) to adjust to the reported environmental changes. I examined changes in environmental factors and species site occupancy between the two study periods and analysed how these environmental changes are related to species niche parameters and their characteristic traits. Since the niche in this analysis was defined by climatic and pollution factors I expect traits related to species flexibility to both resource use (i.e. habitat and diet specialization) and phenological adaptability (i.e. migration status, laying date and length of laying period) to be the key predictors in determining the direction of niche parameters and dynamics.

Overall, generalist species and those with more flexible phenology potential are expected to present wider niche breadths, low marginality indices and higher tolerance. All characteristics that will allow for better niche tracking in case of environmental change. On the other hand species with more constrained traits (e.g. specialist species, migrants) will be characterized by more marginal niches, smaller niche breadth and tolerances that will favour less niche tracking

but potentially promote more markedly range changes in the presence of environmental change.

This constituted one of the first comparative studies that evaluates niche evolution and characteristics in relation to species traits within a single taxonomical clade to try to determine the relation between changes in environmental pressures and the differential responses of target species in terms of their niche characteristics (Losos, 2008).

Finally, I related niche characteristics and dynamics to current risk categories used in UK bird indicators to understand their potential role in improving their application when developing conservation action plans.

5.2 METHODS

5.2.1.Species data

Data on species presence and absence was obtained from the two breeding bird atlases of Britain and Ireland. The first collated data from the period 1968-72 (Sharrock, 1976) and the second from 1988-91 (Gibbons et al, 1993). We refer to these two atlases/time periods as the 1970 and 1990 atlases respectively. For a full account of the methods and concordance between these two periods see Gibbons et al. (1993). Both atlases documented the presence and absence of breeding bird species throughout Britain and Ireland within each 10 by 10 km squared of their national grids. As land cover data and other environmental variables were not available for Ireland and a number of the squares in the British territory, all Irish and incomplete squares were excluded from the analysis (~370 squares). Here, for convenience the geographic area of study is referred to as Britain and includes all islands where data were available. A total of 2357 grid squares were used in the final analysis after

accounting for differences in the squares covered by the two time periods and the extent of the environmental data available. Passerine presence/absence data was available for 82 species and full trait data was accessible for 50 of those species (Table 5.1). A more in detailed description of the trait data is available in Chapter 2 methods.

Table 5.1 Description of species specific traits selected for the niche dynamics analysis

Trait group	***Variable***	**Code**	***Description***
Phenology	Average laying date	ALD	Median date of the 1st egg laying (Julian day)
	Average period of first clutch laying	A1CP	Latest recorded date- earliest recorded date (no. days)
	Migratory status	MS	Nominal variable: Long distance migrant(1) and resident species (0)
Resource use	Diet type	DG	Nominal variable: Omnivorous (1), herbivorous (1), insectivorous (2)
	Woodland as breeding habitat	WBH	Nominal variable: Species with woodland as main habitat during breeding (1), not woodland breeding birds (2)
	Farmland as breeding habitat	FBH	Nominal variable: Species with farmland as main habitat during breeding (1), not farmland breeding birds (2)
Life history	Average body weight	ABW	Average body weight for the species (♀♂)(g)
	Number of brood per year	AB	Average number of clutches per year

5.2.2.Environmental data

Environmental predictors were collated and scaled to the 10km^2 resolution of the species data (Table 5.2). A more detailed description of the four predictors used is available in the methods section in Chapter 3. These four predictors (i.e. February minimum temperature, early breeding precipitation, SO_2 air concentration and PCNM1) were selected as they were not only available for the two time periods but also represented environmental factors that explained a significant portion of the variance observed in the community data as indicated in the previous chapter.

Table 5.2 Environmental predictors used in the niche analysis (i.e. common significant environmental predictors available for the two atlas periods)

Variable group		Predictors	Detail
Abiotic	Climate (2)	Temperature min. Precipitation	February(~pre-breeding conditions) Early breeding (Mar-May)
	Pollution (1)	SO_2 cc	Air concentration of SO_2
Space	Space (1)	PCNM vectors	PCNM1

5.2.3.Statistical methods

Several multivariate analyses were performed to examine the niche characteristics (i.e. position and breath) and of passerine species and their change through time.

Outlying Mean Index (OMI) analysis was used to characterise species niches and to measure the distance between the mean habitat conditions used by each species and the mean habitat conditions of the study area (Dolédec et al, 2000). In OMI analysis the variability of the niche of a species is decomposed into three components: (1) an index of marginality, i.e. a representation of how typical the resource use of the species is compared to the whole community (OMI) and therefore a measure of the species niche position, 2) an index of tolerance or niche breadth, which describes the spatial/ temporal variance of the niche across measured environmental conditions or resources (tol) and; 3) a residual tolerance, i.e. an index that helps to determine the reliability of a set of environmental conditions for the definition of the niche of a species.

Niche parameters (i.e. OMI and tolerance) were extracted using the function *niche* under the 'adehabitatHS' package in R and were used to characterize species niche dynamics (i.e. niche breadth contraction or expansion). Large marginality values represent species with niche positions far from the average environmental conditions of the study area while small values indicate that

species niche are located in areas with close to the average environmental range. In terms of tolerance, species with large tolerance represent species with broad variances along the environmental gradients under study while species with small tolerance values indicate species with restricted gradients along the study environmental factors.

A range index was also calculated as the ratio of the overall occupied squares in the two time periods over the number of occupied squares in either 1970/ 1990. This range index has been shown to reveal an intrinsic property of species that can be thought of as the porosity of a species range (Hurlbert & White, 2007). In this way a species might occupy a small area within the study area and yet have a high value of range index if it occurs in the majority of the sites that it would be expected to occupy according to their environmental requirements (Hurltbert & White, 2007).

Detrended Correspondence Analysis (DCA) was used to obtain estimates of gradient lengths and determine the suitable species environmental response type to apply for subsequent analysis (i.e. length gradient < 2 = linear; gradient length > 3= unimodal response response). Since the correspondent DCA ordination produced gradient lengths of 2.57/ 2.07 and 3.05/ 2.32 for the first two axis of the 1970 and 1990 atlas respectively, and taking into account the scale of the dataset, it was decided Canonical Correspondence Analysis (CCA) was the most suitable procedure for this analysis. First Canonical Correspondence Analysis (CCA) was used to reveal species position and describe bird assemblage and influence of environmental variables in each time period.

To examine the contribution of each environmental factor to community composition, variance partition analysis as described in the previous chapter was used (see Methods in Chapter 3). Since we are interested in the description and quantification of species' niches, the following range of multivariate analyses were used to investigate species niche parameters and

their change between atlas periods. Using CCA with the four environmental variables indicated in Table 3.2 (i.e. those having a significant effect on community composition in both time periods: February minimum temperature, precipitation during early breeding period, SO_2 concentration and PCNM1), the passerine assemblage was summarized for each time period. CCA was especially designed to extract the best combination of environmental variables (synthetic gradients) that maximizes the variance of the weighted average species positions ("niche centroids") (Dolédec *et al.*, 2000). CCA best suits the investigation of the unimodal species responses to the environment (Dolédec *et al.*, 2000) which is what would be expected at this scale for the study bird species.

Using the function *ordiellipse* in the R package 'vegan', the area covered by a 95% confidence limit ellipse was extracted. This ellipse is centred on the species centroid which indicates the average conditions used by the species under the described environmental space. This was done for each time period separately and was considered the third niche parameter representing the niche area for a particular species in either period (1970 or 1990).

Procrustes rotation residuals were the fourth parameter used to determine which species (and sites) were shifting in position within the multivariate ordination space between the two time periods (i.e. degree of range shift). Procrustes analysis scales, rotates and dilates one ordination solution and superimposes it on a second ordination, maximizing the fit between corresponding observations of the two ordination configurations (Mykra *et al.*, 2008). The most commonly used method of Procrustean fitting is based on the least-squares criterion, which minimizes the sum squared residuals (m^2) between two configurations. In this way, Procrustes rotation analysis can be used to examine the degree of inter-period concordance of assemblage patterns. The length of the vector residual represents the lack of fit for an individual species or site between two ordinations with low values indicating strong concordance. Procrustes residuals were extracted using the function

procrustes on the R package 'vegan'. A high Procrustes residual for a species indicates a large shift in its position along one or more of the ordination axes. A high Procrustes residual for a site indicates a square where the environmental conditions have changed to a large degree though only two values in multivariate space are being compared.

Pearson correlation was used to identify which niche parameters (i.e. marginality, tolerance, niche area) and concurrent environmental variables under study (i.e. climate and pollution) were related both in terms of their original state (i.e. 1970 values) and the observed changes over time (i.e. change between 1970 and 1990 conditions).

To investigate which niche parameters were related to species traits, general linear models (GLM) with a stepwise optimal model selection procedure based on corrected AIC (AICc) values were used as described in Chapter 2. Both models for the baseline period (i.e. 1970) and temporal change were developed to look into which species characteristics may be related to both particular niche parameters and their change over time. Interactions between predictors were investigated graphically using coplots.

5.3 RESULTS

5.3.1.Niche parameters and environmental factors

The CCA analysis produced eigenvalues for the first two axes of 0.088 and 0.024 for the 1970 data (total inertia of 0.84) and 0.112 and 0.026 for the 1990 data (Total inertia of 1.08). The models in both cases explained around 14% of the observed variation, and most importantly the direction and effect of the environmental factors in the species ordinations are comparable (Fig 5.3). Axis 1 was dominated by a gradient of high precipitation during the early breeding period (negative) through to and drier conditions associated with elevated and high SO_2 air concentration and February minimum temperatures (positive)

which also correspond to a North South gradient indicated by PCNM1(Fig 5.3). Axis 2 was mainly represented by a February minimum temperature gradient (Fig 5.3).

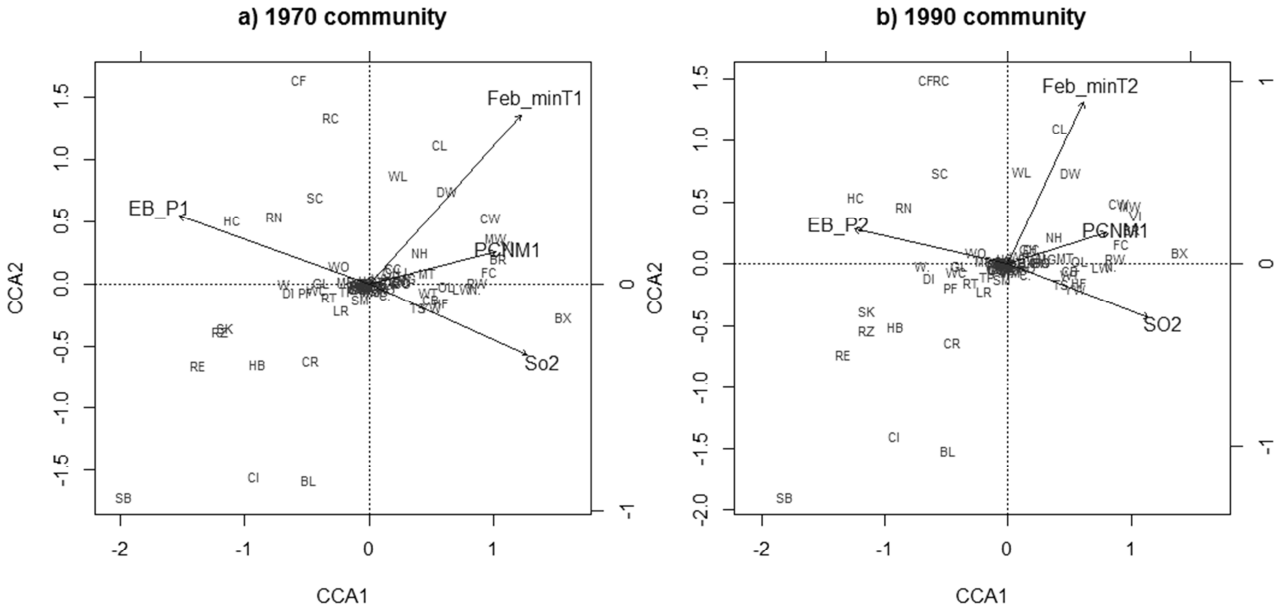


Figure 5.3 Biplots for the 82 bird species community in the British territory studied for the: a) 1970 period, b) 1990 period. Axis one was dominated by the precipitation during the early breeding period (EB_P), air SO_2 concentration (So2) and a North South gradient (PCM1), while Axis 2 represented a February minimum temperature gradient (Feb_min_T). Direction and effect of environmental factors in the two periods are similar and therefore deemed comparable.

Procrustes rotation plots and residuals for both species and squares indicate that significant changes in the centres of species niches and in site conditions have occurred between the two time periods (Fig 5.4). In terms of the species, 20 species had significantly large Procrustes residuals sites (Procrustes

residuals >0.2; Fig 5.4a). However this positional change did not appear to follow a particular pattern, with species shifting along both axes, indicating differential impacts of the environmental factors on species niches (Fig 5.4a). Nevertheless, when looking into the relationship between species Procrustes residuals and the observed environmental changes within the species range, it appears that species presented larger shifts (i.e. larger Procrustes residuals) if significant reductions in SO_2 concentrations and increases in the February minimum temperature had occurred within their ranges (Appendix C).

In terms of squares, the direction of the positional change for the majority of squares (ca. 2100 out of 2357) was in relation to axis2 indicating shifts in relation to February minimum temperature (Fig 5.4b). Nevertheless, when these residuals were plotted against both the square coordinates and the changes in environmental factors in those squares the correlations were notably weak ($r<0.5$; see Appendix C) yet seemed to indicate that the most notable changes occurred on the western and more southern northern latitudes of the study area (i.e. where changes in temperature and pollution might have presented larger effects due to climate change and pollution management plans). In relation to environmental pressures, Procrustes residuals appeared related to decreases in spring precipitation (i.e. early breeding period) and SO_2 air concentrations (see Appendix C).

In relation to the link between species niche parameters and environmental factors, most parameters were associated with early breeding precipitation (Table 5.3). Range index, marginality and niche areas in the baseline period were significantly correlated to precipitation in the same period (-0.8, -0.86 and 0.68 respectively) with species presenting smaller range changes, less marginality and larger niche areas in wetter areas in 1970 (Table 5.3). Marginality and niche area were also correlated to SO_2 and February minimum temperature respectively (-0.73 and -0.74 respectively) with less marginal species in more polluted areas and species with larger niches in warmer locations (Table 5.3). In terms of degree of change, both changes in range and

marginality were correlated with changes in precipitation (0.76 and -0.52 respectively) with smaller range indices and larger marginality associated with reduction in precipitation (0.759 and -0.51 respectively) and increases niche area related to reductions in $SO_{2\ cc}$ (0.58) (Table 5.3).

Table 5.3 Correlation between niche parameters and environmental factors for the baseline period (e.g. 1970) and overall change. Bold figures indicate significant correlations between parameters (p<0.01).

			Environmental factors					
			February minimum temperature		*Early breeding precipitation*		*SO_2 cc*	
			1970	Change	1970	Change	1970	Change
Niche parameters	*Range index*	1970	0.38		**-0.805**		-0.207	
		Change		0.467		**0.759**		0.461
	OMI	1970	0.465		**-0.862**		**-0.731**	
		Change		0.422		**-0.519**		0.172
	Tolerance	1970	-0.313		0.437		0.32	
		Change		-0.004		0.403		0.046
	Niche area	1970	**-0.747**		**0.679**		0.126	
		Change		-0.119		-0.065		**0.584**

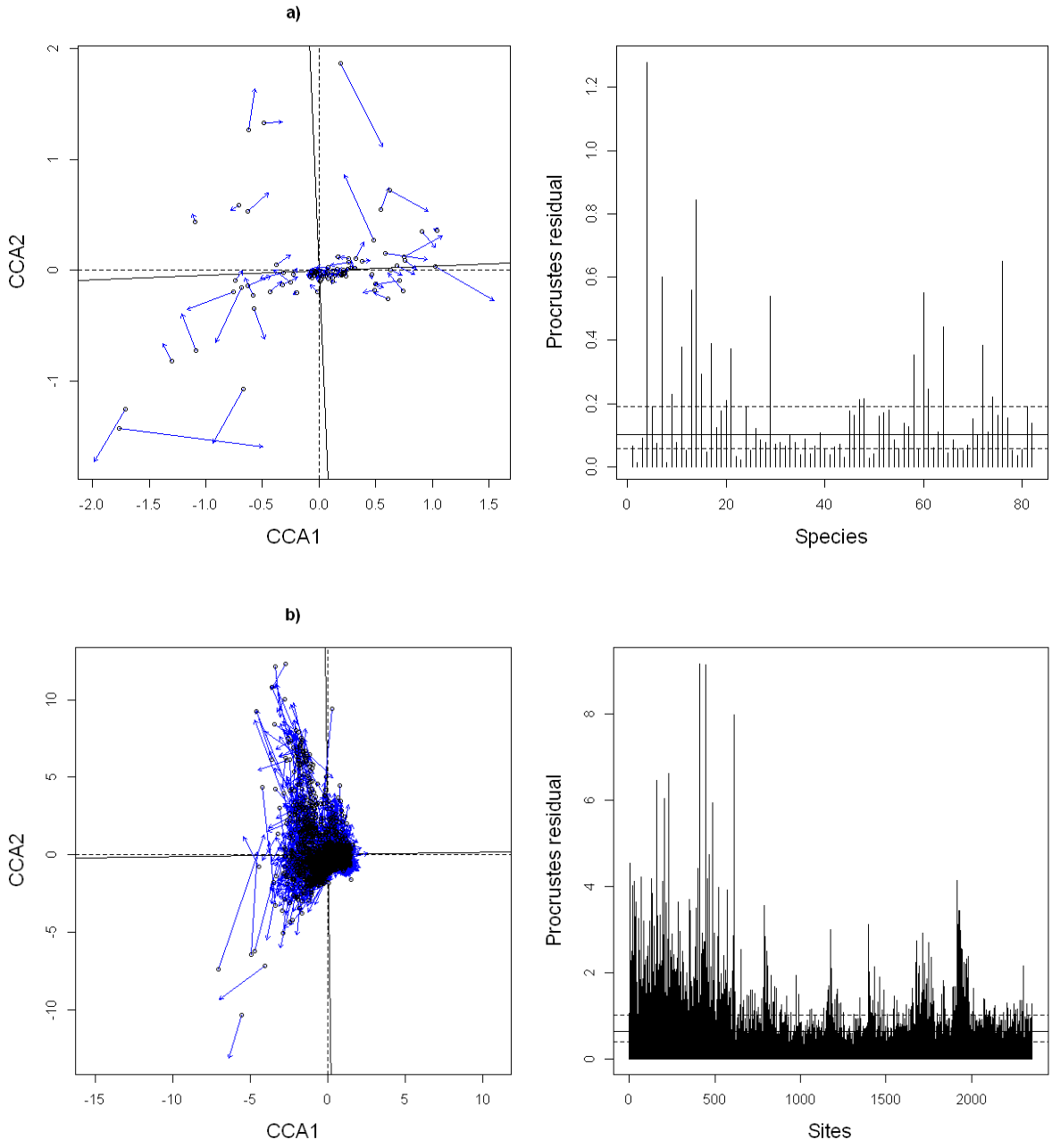


Figure 5.4. Procrustes residuals plots for: a) the 82 passerine species, b) the 2357 sites within the British territory covered in the analysis.

Changes in the range index of species and the changes in the other niche parameters appeared to be significantly related. Changes in the range of species were significantly associated with changes in marginality (r=0.72), Procrustes residuals (r=0.48) and niche area (r=0.38). Furthermore, these

changes in species niche parameters were also associated with concurrent changes in environmental conditions with areas with reduced SO_2 concentration presenting larger shifts in species niche centres (i.e. larger Procrustes residuals , r=0.53).

5.3.2.Niche parameters and species traits

Analysis of the relationship between species niche parameters and species traits revealed significant associations between traits and both baseline niche parameters and their change over the study period. In terms of the relationship between static niche parameters (i.e. niche characteristics in the 1970 baseline period) and species traits; range index, marginality index and niche area were all significantly affected by particular species traits (i.e. best trait-based models with better AIC_c values than their correspondent null models).

In relation to the species range index, the best model explained about 63% of the observed variance in the data (Table 5.4a). Larger species, farmland specialist and those with larger prevalence in the final period presented smaller range indices in this period (Table 5.5a). For species marginality, the best model explained 57% of the observed variance in the data (Table 5.4b). It indicated that species with later laying dates, shorter laying periods, migrants and less prevalent species were more likely to present more marginal niches (Table 5.5b). Furthermore, in terms of the interaction between migratory behaviour and length of the laying period, in residents species those with longer laying periods presented less marginal indices than those shorter ones, while for partial migrants and migrants the opposite trend was true (i.e. species with longer laying periods were more marginal than those with shorter ones) (Fig 5.5). Finally, niche area analysis produced a best model that explained 64% of the observed variance (Table 5.4d). Species with larger body size, higher productivity, earlier laying dates and shorter laying periods, migrants, diet specialist, habitat generalist and more prevalent species were associated with larger niche areas in the 1970 period (Table 5.5d). Also, here the interaction

between migration status and length of the laying period indicated opposite trends for residents and migrants, with residents presenting larger niche areas with longer laying periods and the opposite being true for migrants (Fig 5.6).

Table 5.4 Model performance for niche parameters at baseline period (e.g. 1970) and species traits for the 50 passerine species with fully available datasets: a) range index, b) OMI, c) tolerance, d) niche area.

a) Range index

Model	Variables included	Adj D^2 (D^2)	AIC_c(AIC)	∆AICc
Null	-	0	-139.8	42.8
Saturated	*As* Best + + *Av. No broods/year +Av. 1st clutch laying period + Av. laying date+ Migratory behaviour+ diet type+ Woodland + Av. 1st clutch laying period: migratory behaviour+ Av. Laying date: migratory behaviour*	0.46 (0.69)	-135.6(-168.6)	47
Best	*Av. Body weight + Farmland + prevalence70*	0.60(0.63)	-182.6(-183.5)	-

b) OMI

Model	Variables included	Adj D^2 (D^2)	AIC_c(AIC)	∆AICc
Null	-	0	46.2	24.3
Saturated	*As* Best + *Av. body weight+ Av. No broods/year +Diet type +Farmland +Woodland+ Laying date: migratory behaviour*	0.33(0.62)	61.3(28.3)	39.4
Best	*Av. laying date +Av. 1st clutch laying period+ Migratory behaviour + prevalence70+ Av. 1st clutch laying period: migratory behaviour*	0.48(0.57)	21.9(17.4)	-

c) Tolerance

Model	Variables included	Adj D^2(D^2)	AIC_c(AIC)	∆AICc
Null	-	0	37.4	-
Saturated	*As* Best +*Farmland + Av. Laying date: migratory behaviour+ Av. 1st clutch laying period: migratory behaviour*	0.11(0.37)	77.6(44.6)	40.2
Best	*Av. Body weight+ Av. No broods/year + Av. laying date+ Av. 1st clutch laying period+ Migratory behaviour+ Diet type + Woodland +prevalence70*	0.04(0.27)	47.8(39.4)	10.4

d) Niche area

Model	Variables included	Adj D^2(D^2)	AIC_c (AIC)	∆AICc
Null	-	0	160.3	2.7
Saturated	*As* Best + *Av. Laying date: migratory behaviour*	0.37(0.64)	172.5(139.5)	14.9
Best	*Av. body weight +Av. No broods/year + Av. laying date+ Av. 1st clutch laying period+ Migratory behaviour+ Diet type+ Farmland + Woodland +prevalence70+ Av. 1st clutch laying period: migratory behaviour*	0.42(0.64)	157.6(135.6)	-

Table 5.5 Predictor contribution and performance for best model for niche parameters in the baseline period. Δ AIC_c was calculated by dropping each predictor from the model: a) range index, b) OMI, c) tolerance, d) niche area (Sig. codes: '***' p<0.001 '**'p< 0.01 '*'p< 0.05 '^'p< 0.1).

a) Range index

Explanatory variable (Best model)	Coefficient(SE)	ΔAICc	Posterior probability
	GLM		
Av. Body weight	$-7x10^{-5}(3x10^{-5})$*	3.2	63.7
Farmland specialist	-0.022(0.012)^	1.1	35.9
Prevalence70	$-8x10^{-5}(1x10^{-5})$***	43.2	100

b) OMI

Explanatory variable (Best model)	Coefficient(SE)	ΔAICc	Posterior probability
	GLM		
Av. laying date	0.004(0.003)	0.4	28.6
Av. 1st clutch laying period	-0.003(0.003)	1	2.8
Migratory behaviour(partial migrant)	0.004(0.319)	1	0
Migratory behaviour(migrant)	-0.747(0.344)*		
Prevalence70	$-0.001(8X10^{-5})$***	31.3	100
Av. 1st clutch laying period: partial migrant	0.001(0.005)	1.1	8.4
Av. 1st clutch laying period: migrant	0.013(0.006)*		

c) Tolerance

Explanatory variable (Best model)	Coefficient(SE)	ΔAICc	Posterior probability
	GLM		
Av. Body weight	$-0.001(3x10^{-4})$^	1	8.3
Av. brood number/year	0.243(0.106)*	2.7	48.2
Av. Laying date	-0.011(0.004)*	3.6	7.5
Migratory behaviour (partial migrant)	-0.146(0.133)	1	0
Migratory behaviour (migrant)	0.381(0.18)*		
Diet type (seed eater)	-0.013(0.158)	3.7	0
Diet type (insectivorous)	-0.241(0.142)^		
Woodland specialist	-0.183(0.12)	2	5.8
Prevalence70	$2x10^{-4}(1x10^{-4})$^	0.1	46.3

d) Niche area

Explanatory variable (Best model)	Coefficient(SE)	ΔAICc	Posterior probability
	GLM		
Av. body weight	0.002(0.001)^	22.5	88.5
Av. brood number/year	0.57(0.343)	20.8	29.9
Av. laying date	-0.017(0.011)	20	30
Av. 1st clutch laying period	-0.004(0.013)	19.1	6.3
Migratory behaviour (partial migrant)	-0.359(1.141)	15.7	2.2
Migratory behaviour (migrant)	2.238(1.175)^		
Diet type (seed eaters)	0.597(0.46)	16.2	78.4
Diet type (insectivorous)	0.8(0.376)*		
Farmland specialist	-0.731(0.387)^	19.2	71
Woodland specialist	-0.598(0.373)	17.9	31.8
Prevalence70	$0.001(2x10^{-4})$***	43.3	100
Av. 1st clutch laying period: partial migrant	0.007(0.016)	15.6	21
Av. 1st clutch laying period: migrant	-0.037(0.021)^		

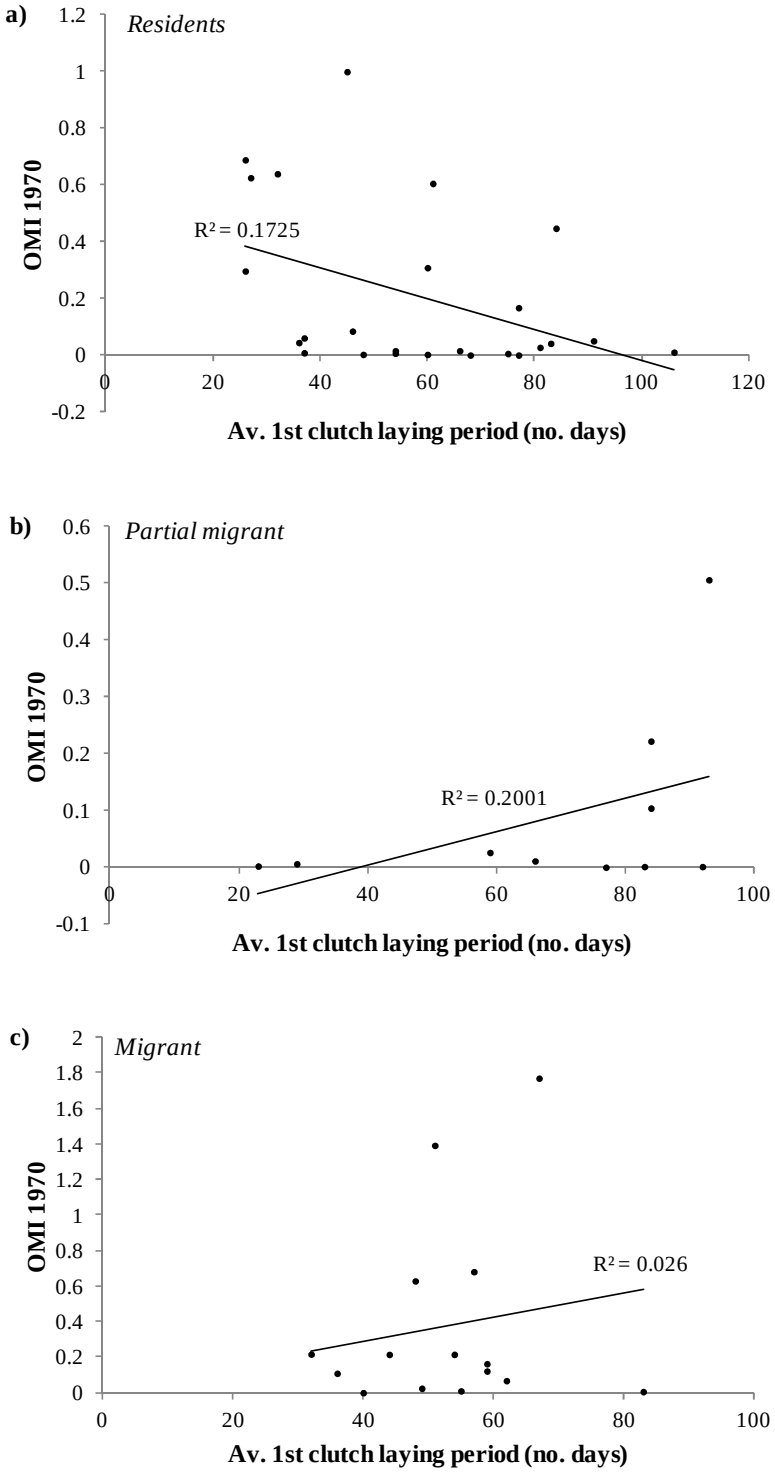


Figure 5.5. Relationship between OMI in the baseline period (i.e. 1970) and average 1st clutch laying period according to species migratory behaviour: a) residents, b) partial migrants, c) migrants.

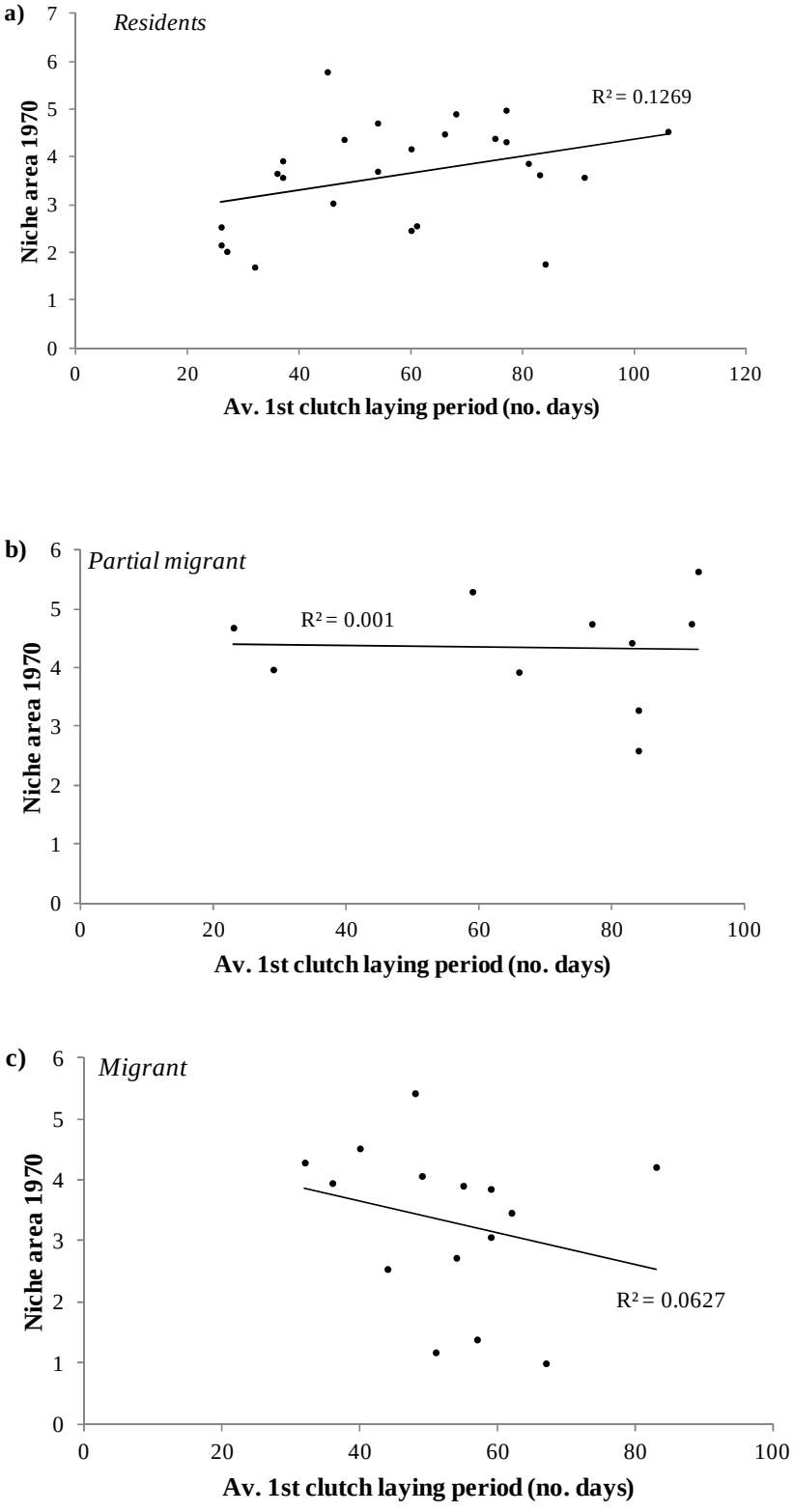


Figure 5.6. Relationship between niche area in the baseline period (i.e. 1970) and average 1st clutch laying period according to species migratory behaviour: a) residents, b) partial migrants, c) migrants

With regards to change in niche parameters and hence species niche dynamics, significant models were produced for changes in range index (i.e. indicative of range shift and therefore niche tracking), tolerance and niche area (i.e. indicative of changes in niche breadth and hence niche dynamics) and a marginal significant model for Procrustes residuals (i.e. also indicative of range shift) (Table 5.6).

The best model for predicting change in range index model explained 61% of the observed variance in the data (Table 5.6a). It indicated that smaller species with later laying dates and longer laying periods, partial migrants and migrants, insectivorous species and habitat specialist, less prevalent species and those species that presented smaller range indices in the baseline period were more likely to suffer from larger range changes (more range shifts) (Table 5.7a). Moreover the interaction between migratory behaviour and phenological traits (i.e. av. laying date), for residents species, those with earlier laying dates presented smaller changes in their geographical range as compared to later laying species (Fig 5.7). This pattern was opposed to that observed for migrant species (Fig 5.7). This patterns were also supported by the Procrustes models (31% of the observed variance) with species with longer laying periods, partial and full migrants and habitat specialists presenting larger residuals (i.e. larger shifts in position) (Table 5.6b, Table 5.7b). As before, the interaction between migratory status and phenological traits presented opposite patterns between resident and migrant species with residents showing larger residuals with longer laying periods and the opposite being true for migrant species (Fig 5.8).

In relation to niche dynamics, both models of change in tolerance and niche area were significant and explained an important part of the observed variance in the data (63% and 35% respectively) (Table 5.6d,e). Changes in tolerance were associated with habitat specialism, prevalence in the later period and the original tolerance level in the baseline period (Table 5.7d). Reduced tolerance (i.e. reduced niche breadth) was associated with farmland specialists, more prevalent species in the 1990 period and those species that presented higher

tolerance values in the baseline period while increased tolerance was observed in woodland specialists (i.e. increased niche breadth) (Table 5.7d). Finally, in terms of change in niche area, the best model for this parameter explained around 35% of the observed variance (Table 5.6e) and showed that larger species, those with later laying dates and less prevalent presented increases in their niche areas (Table 5.7e).

Finally though the model for change in marginality was not significantly better than the correspondent null model (Table 5.6c), it explained about 52% of the observed variance in the data and presented interesting relationships between a number of species traits (Table 5.7c). Increases in marginality were associated with large body size, later laying dates, shorter laying periods, partial and full migrants, insectivorous species, farmland specialists and species that presented smaller marginality values in the baseline period (Table 5.7c). Furthermore, interactions between migratory status and phenological flexibility traits revealed again opposite trends between resident and migrant species with residents presenting increases in marginality with later laying dates and longer laying periods and the opposite being true for migrant species (Fig 5.9 and 5.10).

Table 5.6 Model performance for change in different niche parameters and species traits for the 50 passerine species with fully available datasets: a) change in range index, b) Procrustes residuals, c) change in OMI, d) change in tolerance, e) change in niche area.

a) Change in range index

Model	Variables included	Adj D^2 (D^2)	AIC_c(AIC)	∆AICc
Null	-	0	-30.23	1.66
Saturated	*As* Best + *Av. 1st clutch laying period+ Av. No broods/year+ Av. 1st clutch laying period: migratory behaviour*	0.26 (0.59)	-8.46(-45.94)	23.43
Best	*Av. Body weight+ Av. laying date+ Migratory behaviour+ diet type+ Farmland +Woodland + prevalence 90+ range index 1970+ Av. Laying date: migratory behaviour*	0.41(0.61)	-31.89(-51.02)	-

b) Procrustes

Model	Variables included	Adj D^2 (D^2)	AIC_c(AIC)	∆AICc
Null	-	0	-150.5	-
Saturated	*As* Best *+Av. body weight + Av. laying date+ Av. No broods/year +Diet type +Woodland+ Laying date: migratory behaviour+*	0 (0.44)	-112.12(149.6)	38.38
Best	*Av. 1st clutch laying period+ Migratory behaviour+ Farmland + prevalence 90+ Av. 1st clutch laying period: migratory behaviour*	0.131(0.31)	-149.26(-154.9)	1.24

c) Change in OMI

Model	Variables included	Adj D^2(D^2)	AIC_c(AIC)	∆AICc
Null	-	0	-31.89	-
Saturated	*As* Best + *Av. No broods/year + Woodland*	0.16(0.54)	-0.82(-38.3)	31.7
Best	*Av. Body weight+ Av. laying date+ Av. 1st clutch laying period+ Migratory behaviour+ Diet type+ Farmland +prevalence 90+ OMI 1970+ Av. Laying date: migratory behaviour+ Av. 1st clutch laying period: migratory behaviour*	0.22(0.52)	-15.46(-40.79)	16.43

d) Change in tolerance

Model	Variables included	Adj D^2(D^2)	AIC_c (AIC)	∆AICc
Null	-	0	-2.58	40.43
Saturated	*As* Best *+Av. body weight +Av. No broods/year + Av. laying date+ Av. 1st clutch laying period+ Migratory behaviour+Diet type+ Av. Laying date: migratory behaviour+ Av. 1st clutch laying period:migratory behaviour*	0.41(0.67)	11(-26.48)	54.01
Best	*Farmland + Woodland +prevalence 90+ tolerance 1970*	0.58(0.63)	-43.01(-44.96)	-

e) Change in niche area

Model	Variables included	Adj D^2(D^2)	AIC_c(AIC)	∆AICc
Null	-	0	-127.9	14.7
Saturated	*As* Best + *Av. 1st clutch laying period+ Migratory behaviour+ Farmland +Diet type+ Av. No broods/year +Woodland+ Av. Laying date: migratory behaviour+ + Av. 1st clutch laying period: migratory behaviour+ area 1970*	0(0.386)	-84.42(-121.9)	58.2
Best	*Av. body weight +Av. laying date+ prevalence 90*	0.3(0.345)	-142.6(-143.1))	-

Table 5.7 Predictor contribution and performance for best model of changes in niche parameters. Δ AIC_c was calculated by dropping each predictor from the model: a) change in range index, b) procrustes residuals, c) change in OMI, d) change in tolerance, e) change in niche area (Sig. codes: '*' p<0.001 '**'p< 0.01 '*'p< 0.05 '^'p< 0.1).**

a) Change in range index

Explanatory variable (Best model)	Coefficient(SE)	ΔAICc	Posterior probability
	GLM		
Av. Body weight	-0.0003(0.0001)	0.5	6.3
Av. Laying date	0.008(0.002)^	2.6	92.8
Migratory behaviour (partial migrant)	0.692(0.41)***	3.1	1.9
Migratory behaviour (migrant)	1.063(0.492)^		
Diet type (seed eater)	-0.11(0.063)*	4.6	7.9
Diet type (insectivorous)	0.043(0.056)^		
Farmland specialist	0.079(0.06)	4.7	9.2
Woodland specialist	0.076(0.058)	4.7	6.4
Prevalence70	-0.0003(0.0001)***	20	100
Range index 70	-1.413(0.557)*	3.4	96.6
Av. laying date: partial migrant	-0.006(0.003)^	1	16.5
Av. laying data: migrant	-0.009(0.004)*		

b) Procrustes

Explanatory variable (Best model)	Coefficient(SE)	ΔAICc	Posterior probability
	GLM		
Av. 1st clutch laying period	0.093(0.031)	1.1	9.6
Migratory behaviour (partial migrant)	0.052(0.056)^	2.2	0
Migratory behaviour (migrant)	0.122(0.061)		
Farmland specialist	0.033(0.017)^	0.4	41.3
Prevalence 70	$4x10^{-4}(1x10^{-4})$**	6	94.5
Av. 1st clutch laying period: partial migrant	-0.001(0.001)	1.4	13.5
Av. 1st clutch laying period: migrant	-0.001(0.001)*		

c) Change in OMI

Explanatory variable (Best model)	Coefficient(SE)	ΔAICc	Posterior probability
	GLM		
Av. body weight	$4x10^{-4}(1x10^{-4})$*	2.8	5.5
Av. laying date	0.008(0.002)**	3.3	27
Av. 1st clutch laying period	-0.001(0.002)	3.3	5.3
Migratory behaviour (partial migrant)	1.106(0.457)*	0.2	15.4
Migratory behaviour (migrant)	1.36(0.547)*		
Diet type (seed eaters)	-0.097(0.083)	7.3	0
Diet type (insectivorous)	0.056(0.06)		
Farmland specialist	0.139(0.056)*	0.2	30.8
Prevalence 70	$-1x10^{-4}(6x10^{-6})$*	2.1	26
OMI 70	-0.158(0.085)^	0.6	17.3
Av. laying date: partial migrant	-0.01(0.004)*	3	25.9
Av. laying date: migrant	-0.009(0.004)^		
Av. 1st clutch laying period: partial migrant	0.001(0.003)	8.8	27.4
Av. 1st clutch laying period: migrant	-0.006(0.004)		

d) Change in tolerance

Explanatory variable (Best model)	Coefficient(SE)	ΔAICc	Posterior probability
	GLM		
Farmland specialist	-0.13(0.059)*	2.1	79.1
Woodland specialist	0.072(0.051)	0.9	41.3
Prevalence 70	$-1x10^{-4}(4x10^{-6})$***	10.9	98.5
Tolerance 1970	-0.463(0.063)***	36.6	100

e) Change in niche area

Explanatory variable (Best model)	Coefficient(SE)	ΔAICc	Posterior probability
	GLM		
Av. Body weight	0.0002(0.0001)***	11.7	97.3
Av. Laying date	0.001(0.0005)*	3.7	54.6
Prevalence 70	$-3x10^{-4}(2x10^{-5})$	0.8	35.7

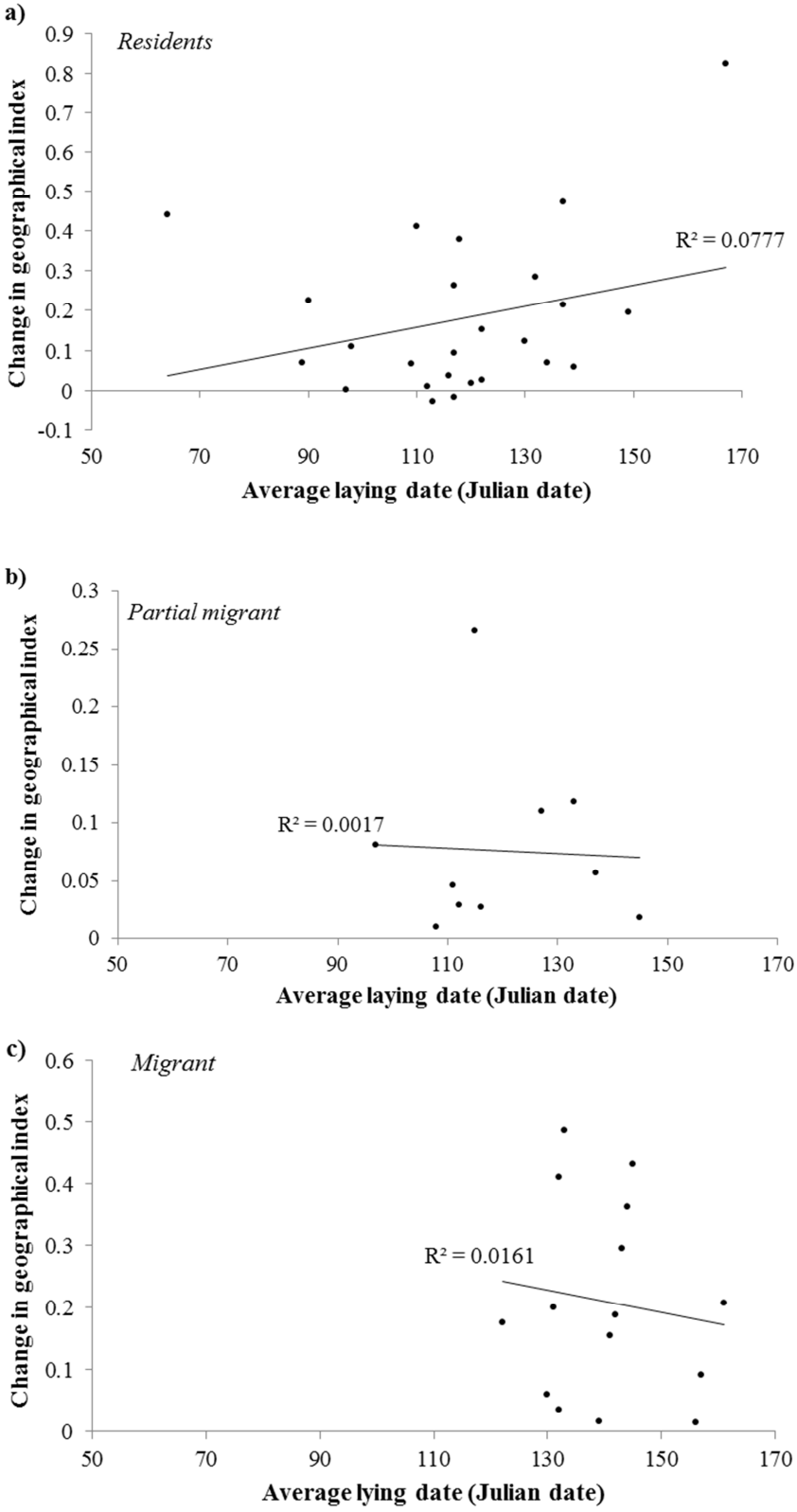


Figure 5.7. Relationship between change in range index and average laying date according to species migratory behaviour: a) residents, b) partial migrants,c) migrant

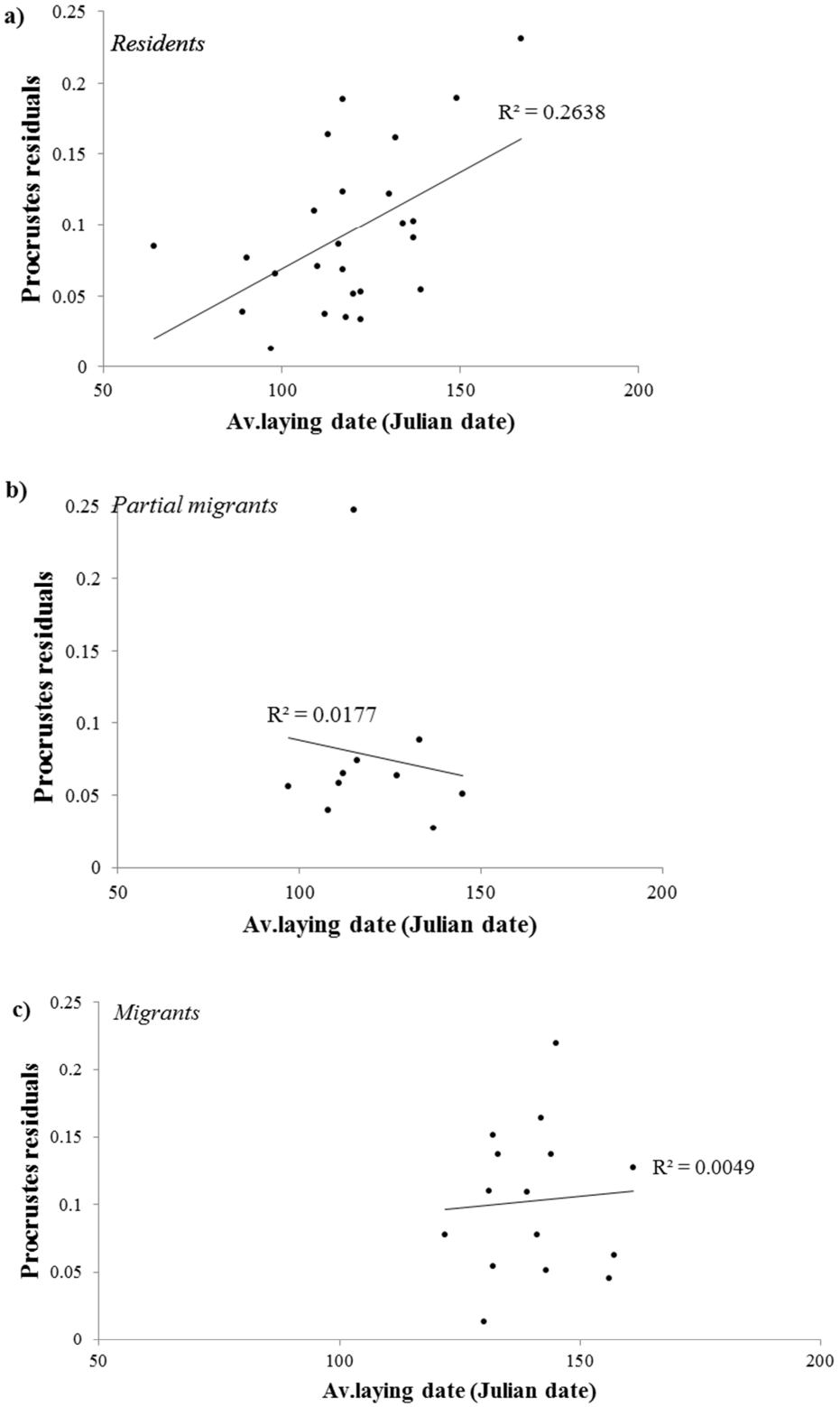


Figure 5.8. Relationship between Procrustes residuals and average 1st clutch laying period according to species migratory behaviour: a) residents, b) partial migrants, c) migrants

5.4 DISCUSSION

This is one of the first studies to have attempted to describe both (a) species niches using a variety of descriptive parameters and (b) niche parameter changes over time using a multivariate analytical framework. This approach, as applied here, allowed for the extraction of different niche metrics (i.e. Procrustes residuals, OMI, tolerance and niche area), that can be used to measure various aspects of a species niche explicitly and its change over time. This approach allowed the following ecological hypotheses to be tested: 1) are processes of niche evolution/ niche conservatism occurring within the UK passerines?, 2) which environmental pressures are driving the observed changes in species' niche parameters and which of those are most affected?, 3) are there any species traits that explained the differential responses of niche dynamics observed in species?, 4) is there any relationship between the observed niche dynamics and change in parameters and the current UK conservation categories?

5.4.1.Overall role of environmental change in niche dynamics

Environmental conditions, including climate (temperature and precipitation) and pollution variables, changed across sites when comparing the passerine assemblages of 1970 and 1990. Though the correlations were weak they appear to corroborate environmental change reported for the region in other studies (Perry, 2006). The key climatic trends identified were: a) a general increase in temperature (~1ºC), particularly since 1987, with minimum temperatures showing a much larger increase than maximum temperatures and b) significant increases in overall precipitation since 1961 with winter precipitation increasing dramatically in the West of the UK (Perry, 2006). In terms of pollution, it has been reported that atmospheric concentrations of sulphur dioxide and nitrogen oxides have now declined to levels which do not longer pose a direct toxic threat from their peak levels in 1970s (RoTAP, 2012). These pollutants have been shown to have detrimental effects on bird populations such as eggshell thinning and reduced egg mass due to the

increased acidification of habitats (e.g. Ormerod et al., 1988). This study suggested relatively weak observed relationships between changes in pollution and species niche dynamics. It is likely that this could be due to the large-spatial scale of the study masking small-temporal changes, as is likely for local impacts of pollutants and the relatively short time period between time-periods.

The fact that we can report a change in the overall environmental conditions between the two time periods sets the scene to investigate the processes of species niche tracking and niche dynamics in relation to these changes.

In fact, as reported in Chapters 3 and 4, species niche characteristics were closely associated with the concurrent environmental factors under study with species presenting significant correlations between both baseline values and overall change. The results provide further evidence that species react to changes in their environment and that these can be traced through changes in their niche characteristics. Furthermore, the fact that most niche parameters change were associated with changes in precipitation and pollution support previous studies that report species modifying their behaviour and/or condition in response to these factors. For example, Anglier et al (2011) reported that female American redstarts (*Phoenicurus phoenicurus*) present changes in their body condition in response to changes in precipitation in their study areas while Crick and Sparks (1999) reported changes in the laying date of species in relation to both changes in temperature and rainfall. Newman et al. (1985) has also reported low abundances and poor breeding success in house martins (*Delichon urbica*) as a response to variations in insect abundance caused by air pollution.

5.4.2.Niche tracking and niche dynamics in relation to species traits

A number of species changed their position significantly in ordination space (i.e. significant values of Procrustes residuals) and geographical range between the two time periods, indicating evidence for niche tracking in a community setting.

This result echoes that of Tingley *et al*. (2007) who demonstrated that bird species tracked changes in temperature and precipitation. Here, niche tracking (shift in position between the two time periods) was significant for 1/3 of the species studied. Furthermore, the direction of these changes (i.e. direction of Procrustes residual vectors), was mainly associated with concurrent changes in pollution levels and February minimum temperature between the two time periods. Species in areas where either pollutant concentration had significantly decreased or where the minimum temperature had increased have moved position (larger Procrustes residuals) appreciably. This could be taken as an indication of the species tendency to move in order to track suitable conditions that match their environmental requirements, hence providing evidence for lack of adaptability to new conditions and hence inability to track niche changes..

These results corroborate what would have been expected from niche tracking theory in terms of species spatial shifts as conditions in their occupied areas become unsuitable for their optimal survival (Tingley et al., 2007; Pearman et al., 2007). Those species that demonstrated this tendency to follow optimal conditions were associated with traits such as migrant behaviour (i.e. partial and full migrants), habitat specialist (i.e. farmland species) and phenological plasticity (i.e. length of the laying period).However, there was also evidence of species presenting niche tracking (i.e. small Procrustes indices and small changes in rage index) and being able to adapt to new conditions in their environment. For example, resident species with earlier laying dates or non-specialist species were characterized by smaller Procrustes indices and smaller changes in range index.

Resident species would be able to gather cues from their environment throughout the year hence allowing them to respond to changes in a more immediate manner. Those species with earlier laying dates should be able to adapt better to changes in local temperature and take advantage of being able to track changes as their occur in their breeding areas while species with later laying dates may be worse prepared to adapt . On the other hand, migrants do

not have the advantage of being able to trace local conditions in the breeding grounds, and hence the flexibility o their phenological traits will be even be more crucial to their ability to track niche changes. For example, those migrants species that have earlier laying dates and longer laying periods should be more able to adapt to the changing conditions in the breeding environments even when they are cannot use local cues to track environmental changes. However, species with later laying dates and shorter laying periods will be forced to shift spatially towards the optimal conditions for their breeding range as they are limited in terms of time available for their reproduction.

Species marginality was influenced by traits associated with species phenological flexibility (i.e. migratory status, laying date and length of laying period); species with later laying dates and shorter laying periods were more marginal than those with earlier and longer characteristics respectively. Moreover, migrant species were more likely to show an increase over time in their marginality values as compared to partial or resident species, suggesting that they are not able to track environmental changes in the breeding grounds. Species with both specialized habitat and diet presented increased marginality values; restricted resource use renders species more sensitive to environmental changes. This is particularly relevant for insectivorous species as prey abundance is likely to respond to environmental cues more quickly than bird breeding phenology, with the result that peak prey abundance will no longer match the optimal timing for insectivorous species breeding cycles (Carey, 2009).

Changes in niche breadth (i.e. tolerance), were associated mainly with habitat specialization. However, the direction of the changes varied across habitats. Niche breadth in farmland specialists reduced over time, whereas niche breadth increased in woodland species. These results may be indicative of the different management practices that each of this land uses have experienced during the time period under study. While farmland areas underwent a significant decrease in area coupled with an increase in the intensity of production (more intense

farming, loss of fallow land, etc), woodland and forested areas experienced a significant increase in cover and protection due to replanting of coniferous and broadleaf species (UKNEA, 2011). Therefore, the quality and availability of resources for the species associated with these two habitat types may have changed in opposite directions.

Finally, the results for niche area mirror those presented for niche breadth, with larger, more-common species, and those with a potential for earlier laying periods appearing more likely to expand their areas as they present the most adequate characteristics to favour this process (adaptation to changing environment, and enough population sources to expand their range).

Overall, this study has demonstrated that both niche tracking and niche dynamics are both processes well integrated in the community dynamics of passerine species within the study area. As it has been reported in the previous chapters, both niche characteristics and their change can be linked to concomitant change in environmental factors. Thus, there is the potential to use or include them as part of the next generation of biodindicators. However, is worth keeping in mind the broad scale of this study and that further studies looking into these niche dynamics processes across a range of scales may help identify stronger patterns between species responses (in terms of niche parameters), key environmental pressures and species traits.

Finally, the fact that niche evolution has been demonstrated across a number of passerine species indicates that assumptions about the static nature of niche characteristics assumed in many species distribution models are not necessarily valid and should be adequately addressed in the development and application of these methods (Araujo & Guisan, 2006).

Chapter 6 : Regional extinction and colonisation in UK passerines

ABSTRACT

Understanding the biological traits associated with range decline is a fundamental step for predicting and mitigating extinction risk. Evaluating small-scale changes in distribution patterns over time can identify these traits. This chapter evaluates patterns of colonisation and extinction in the UK passerine community to try to determine which the main environmental drivers of range change over time. The analytical framework allows for the simultaneous analysis of environmental factors, species traits and their interactions. Extinction and colonisation processes were associated with species phenology, specialisation and migratory behaviour. Migrant species with more flexible phenology, higher productivity and more generalist ecology were more likely to colonise new areas. Range changes were strongly predicted by interactions between these species-specific traits and environmental change. Thus, in order to accurately predict species responses to environmental change, it is necessary to incorporate interactions between species biology and environment.

6.1 INTRODUCTION

Mitigating extinction risk is a fundamental conservation priority (Convention on Biological Diversity, 2010). The spatial and temporal distribution of species results from dynamic processes of extinction and colonization that determine the overall area of occupancy of a species (Gaston & Blackburn, 2002). Both processes occur across the distributions of most species, although colonisations will predominate for species expanding their range and extinction for species whose range is contracting (Gaston & Blackburn, 2002). In the case of highly mobile groups such as birds, such changes can occur very rapidly (Gates & Donald, 2000). Therefore, it is only by understanding which factors

drive distribution changes that we can make predictions of future species responses to environmental change.

Both extrinsic and intrinsic factors can affect the likelihood of extinction or colonisation processes occurring. Extrinsic factors such as global climate and land-use changes have been of major scientific and political concern (Barbet-Massin et al., 2012). Climate is often assumed to be one of the main drivers of bird distributions at large spatial scales (Jimenez-Valverde et al., 2011) with changes in climatic conditions expected to produce shifts in species if the individuals are able to track climate changes either spatially or temporally (Barbet-Massin et al., 2012). For example, analyses of data from nesting dates in UK (NRS; Crick et al., 2003) showed that 20 species exhibited statistically-significant trends towards earlier laying and that this was related to changes in temperature or rainfall (Crick & Sparks, 1999; Robinson et al., 2007). Climatic changes will be particularly disruptive if they occur during the most vulnerable periods of the species life cycle, for example in birds conditions during overwintering and/or breeding periods would be crucial for species survival and fitness in terms of their effects on mortality and productivity (Cricks & Sparks, 1999; Robinson et al., 2007).

Land use and land cover changes affect biodiversity worldwide (Jetz et al., 2007). These changes are expected to present significant effects for terrestrial ecosystems at the landscape level (Lee & Jetz, 2011). The most commonly considered change is conversion of forest and grassland habitats into cultivated or urban land (de Chazal & Rounsevell, 2009). When land cover is transformed into different types or uses, then suitable habitat for some species may be reduced. This habitat loss has been linked to declines in number of specialist and large bodied species (Gibbs & Stanton, 2011) and also reduced breeding success (Kurki et al., 2000). For example, the decline in corn bunting (*Miliaria calandra*) populations in the UK has been linked to the increase in agricultural intensity and mechanization that has led to losses of spring tillage and declines in the area of winter stubbles (Donald, 1997).

Both climate change and land use change are therefore key drivers of biodiversity change (Travis et al., 2003; de Chazal & Rounsevell, 2009). However they rarely work in isolation, with complex interactions between environmental changes that appear to have greater effects than might be expected from their independent contributions (Root & Schneider, 2006; Brook, 2008). For example, a study carried out by Sala et al. (2005) concluded that number of vascular plant species and their abundance may decrease by 12-16% by 2050 relative to species present in 1970 due to the synergic effects of climate change, land use change and nitrogen deposition.

Other factors that can potentially impact species extinction and colonisation rates could be biotic factors such as competitors or predators (White et al. 2008; Wisz et al., 2013). UK raptor numbers significantly declined during the first half of the 20th century due to human persecution and intense pesticide use. However, since the introduction of pesticide regulations and the Bird Directive there has been a considerable increase in their numbers, particularly in areas where other birds were previously thriving. Hence, it has been suggested that predation rates may have a significant impact on bird populations in areas where their main foraging or nesting habitat structure has been notably altered and/or where predation pressure has significantly increased (Whittingham & Evans, 2004).

Apart from extrinsic factors driving extinction and colonisation processes, there are also intrinsic factors related to species traits that would represent the vulnerability or sensitivity of species to external threatening processes (Cardillo et al., 2008). Species-specific traits will lead to some species being competent colonisers whereas others will be more extinction prone. Some common predictions about species traits that correlated to vulnerability to extinction are as follows (Purvis et al., 2000):

- Small populations are more likely to disappear due to processes such as demographic stochasticity, slow rates of adaptation or inbreeding. Hence small geographical ranges and low population abundances are likely to confer an enhanced extinction risk.
- Endemic species present both the above mentioned characteristics besides a particular vulnerability to competitors and predators that will make them even more susceptible to introduced species and overexploitation.
- Higher tropic level species will be more vulnerable to the cumulative effects of disturbance at lower levels.
- Species with 'slow' life histories (i.e. small litters, slow growth rates, long gestation…) would be less able to compensate for increased mortality through increases in fecundity and therefore would be more vulnerable to extinction.
- Species with large home ranges would be particularly vulnerable to habitat loss and degradation and hence edge effects.
- Large body size correlates with extinction promoting traits with larger species having low population densities, slow life histories and larger home ranges.

Ecological and life-history traits have already been associated with extinction risk in comparative studies (Reynolds et al., 2005). Avian species traits can be subdivided into three groups: life-history (i.e. body weight, productivity), phenological (i.e. laying date, clutch laying period, migration strategy) and resource-use traits (i.e. habitat dependency, diet group). It has already been reported that large bodied species, habitat specialist and long distant migrants are facing larger population declines in Europe due to both land-use and climatic changes (Julliard et al, 2004; Gregory et al., 2005; Cardillo et al., 2005; Salido et al 2012; Van Turnhout et al 2010). Traits associated with species vulnerability are expected to show high probability of extinction. Body mass has been linked to increase extinction probabilities due mainly to the tendency of body mass to be negatively related to population size. However in passerines,

body mass has been positively associated with increased population trends (Salido et al., 2012), hence we predict larger species to be less likely to go extinct but also less likely to colonise new areas. Conversely, traits associated with dispersal ability such as high productivity and ecological flexibility should be associated with larger colonisation rates. In terms of productivity, species with multiple broods during the year could present larger colonisation rates and smaller extinction rates as they would be able to compensate their losses through the breeding season by producing broods later in the season. Also generalist species that can use a variety of resources (i.e. habitat or diet) or those that relying of non-seasonal food items are expected to be less likely to present high extinction rates. For example, species with later laying dates and longer laying periods should be more likely to colonise and less likely to go extinct, whereas insectivorous and migrant species may present larger extinction rates due to the effect of timing mismatches during key parts of their breeding periods.

Also species prevalence/occupancy will have a significant effect on the rates of species colonisation and extinction (Doxford & Frekleton, 2012). In general, rare sparsely distributed species would normally be more vulnerable to extinction processes and would be less likely to colonise with the opposite being true for widespread, densely distributed species (Doxford & Frekleton, 2012; Preston, 2000; Wilson et al. 2004). Therefore, species responses to the various characterisations of climate change and land-use change vary considerably depending on which species are considered. Furthermore, the way each species responds to each driver, will be different whether there are any interactions between drivers, species and the spatial and temporal scale considered (de Chazal and Rounsevell, 2009). Some of these interactions would be quite intuitively. For instance, phenological traits (i.e. migration behaviour, laying date and laying period) would have significant importance on the ability of species to respond to climatic changes. In the case of species with earlier laying dates these will be more likely to perform better in areas where climate change has promoted an advance in spring dates.

In order to look into this species trait-environment relationship, comparative models are required. Historical presence/absence distribution records are useful in developing general predictions of large-scale dynamics as they provide a long-term perspective (Doxfrod & Frekleton, 2012). Using distribution data at multiple discrete time points allows an assessment of how environmental factors and species characteristics contribute to species distribution changes and could help identifying the main drivers of these processes (Doxfrod & Frekleton, 2012; Gaston & Blackburn, 2002). By identifying the main extrinsic factors driving colonisation and extinction dynamics in species and the particular characteristics associated with this vulnerability or resilience to external factors, species based prioritization for potential conservation actions can be established.

Apart from this, comparative studies of extinction and colonisation can provide also the baseline data needed to assess the current threat status of species (i.e. International Union for Conservation of Nature (IUCN) Red List) or at least identify threatened ecosystems, species or habitat types (Cardillo et al., 2012). Ultimately the aim would be to expose the relative importance of different threat types and how they interact with biological traits to elevate extinction risk of species (Cardillo et al., 2012). For example, Owens and Bennet (2000) showed that among bird families, habitat specialists are more likely to be threatened by habitat loss while large bodied species are more likely to be threatened by overexploitation.

This study aims at evaluate the extinction and colonisation events in UK passerines with two main objectives: i) to identify environmental characteristics that best predict the rates of local colonisation and extinction over the time period between the two national surveys, ii) to determine suites of traits associated with high rates of extinction and colonisation. In terms of driver trait interactions it is expected that: i) species with more flexible phenological traits (i.e. partialmigratory species, extended laying periods or advance laying dates) will present smaller extinction rates and larger colonisation rates in warmer

areas and the opposite in the case of more restricted species, ii) species with more generalist diets will be more able to adapt to changes compared to more specialitazed species as climate change affects resource availability, iii) species using more exposed habitats (e.g. farmland species) to be more at risk of predation than those in more protected habitats (e.g woodland species).

The main novelty in this approach being that the identification of environmental driver and species traits is made simultaneously and not sequentially and that interactions between these extrinsic and intrinsic factors are explicitly analysed in the modelling framework.

6.2 Methods

6.2.1.Species data

Species data were extracted from the two British breeding bird atlases for the periods 1968-72 (Sharrock, 1976) and 1988-91 (Gibbons et al, 1993). The data were used to map, for each census period separately, the presence or absence in each 10 x 10 km^2 British National grid square of all bird species recorded breeding in Britain. Although the two atlases were not generated using identical methodologies their data are suitable for comparative studies (see Gibbons et al, 1993 for details and discussion). As environmental data was not available for Ireland and a number of the British territory squares, all these incomplete records were excluded from the analysis (~370 points). This meant 2358 grid squares for the UK territory were available and for 50 passerine species with accompanying biological trait data.

A set of traits was obtained for each species (Table 6.1). Some traits were expected to act independently on extinction and colonisation rates regardless of the environmental context due to their inherent effect on species fitness (i.e. body weight). However most species characteristics included a range of ecological and phenological traits that might influence species extinction and

colonisation rates due to impacts on their performance along environmental gradients (Violle et al., 2007).

Table 6.1. Species traits used in the extinction and colonisation

Trait group	Variable	Description	*Source*
Phenology-related	Average laying date	Median date of the 1st egg laying (Julian day)	Robinson (2005) (http://blxl.bto.org/birdfacts).
	Average period of first clutch laying	Latest recorded date-earliest recorded date (no. days)	Robinson (2005) (http://blxl.bto.org/birdfacts).
	Migrating status	Migrant, partial migrant and resident	Dudley et al. (2006)
Ecological	Diet type	Generalist, seed eaters, insectivorous	Snow and Perrins(1998) BWP
	General Habitat	Farmland species, woodland species	Newson et al. (2004) Siriwardena et al (1998), Gregory et al (2007), Snow & Perrins (1998). BWP
Life history	Average body weight	Average body weight for the species (♀♂)(g)	Snow & Perrins (1998). BWP
	Average number of brood per year	Average number of clutches per year	Snow & Perrins (1998). BWP

In order to account for the properties of the species distributions themselves, the number of occupied grid squares per species was tallied and species prevalence in the 1988-91 atlas calculated (proportion of grid squares occupied). This was done to deal with an unavoidable negative correlation between species' prevalence (occupancy rate) and extinction and a positive correlation between prevalence and colonisation (Blomqvist et al, 2003). Thus the overall prevalence of each species in the 1990 data was included in the analysis (Blomqvist et al., 2003).

It was predicted that species occupancy and the proximity of neighbouring populations will also have a major role with more prevalent species and those with a higher density of surrounding occupied cells (cf Cook et al. 2007) will present higher colonisation rates and lower extinction rates.

6.2.2. Environmental gradients

Data on regional-scale environmental gradients were compiled from GIS databases as indicated in Table 6. 2.

Table 6.2. Environmental variables used in the extinction and colonisation models

Variable group (number of variables)	Original resolution	Predictors	Details	Source
Climate (2)	5 km^2	Minimum Temperature	Average February temperature in 1990, and change in average February temperature (~pre-breeding conditions)	UKCIP
Biological (1)		Predator number	Change in number of predator species per grid square	Breeding bird atlas data 1968-71 and 1988-91

UKCIP data was used to calculate the mean 1960-1990 minimum temperature during February, which we assumed represented climatic conditions during the pre-breeding season and determined both the conditions for the peak growing season and the pre-breeding conditions of birds. Also the number of predator species per square grid was calculated to estimate the potential impacts of this biological extrinsic factor.

We also included a spatial variable (lambda) that relates to structure and the distance of a particular cell to other occupied squares in the first time period given by the following function:

$$Lambda = exp^{(-0.15 * distance)}$$

High values are obtained when cells are completed surrounded by cells occupied by the focal species within a neighbourhood of radius 60km and low values when no occupied cells occur within this neighbourhood. In this analysis we used a variety of lambda values that represented a range of neighbourhood radius (from 10 to 60), though the best fitted lambda for both colonisation and extinction models was that corresponding to buffer distance of 30km (Table 6.3).

Table 6.3. Model parameters for the different lambda values in relation to, a) colonisation rate, b) extinction rate.

a)

	no lambda	Lambda3	lambda2	lambda1.5	lambda1
range (km)	0	10	20	30	40
AIC	22555	18952	18775	18694	18698
AUC	0.735	0.844	0.848	0.85	0.85
Rsqr	0.153	0.337	0.346	0.35	0.349

b)

	no lambda	lambda3	lambda2	lambda1.5	lambda1
range (km)	0	10	20	30	40
AIC	67301	63454	63214	63097	63110
AUC	0.759	0.794	0.796	0.797	0.797
Rsqr	0.186	0.251	0.255	0.257	0.257

Considering the scale of the study, it is expected that the highest probability of extinction/colonisation will be observed in areas of intense climate change. Considering the recent increase of temperatures and the consequent advancements in seasons (particularly spring) and freezing risk we predict increased extinction rate in warmer areas. Furthermore, we expect that with the

recent increases in raptor abundance there will be an increased species declines due to predation and therefore a significant increase in extinction and colonisation events.

6.2.3. Modelling approach

We examined whether interactions between species' traits and environmental factors influenced patterns of extinction and colonisation between 1968-71 and 1988-91. Extinction and colonisation events were identified as disappearance or appearance of species from the grid squares in the UK territory. Thus, the outcome of each species in each grid square was classified as extinct (present in 1968-71, absent in 1988-91), persisting (present in both atlas periods), colonised (absent in 1968-71, present in 1988-91) or failed to colonise (absent in both atlases). However, for brevity we refer to the data as extinction/persistence and colonisation/failure.

These rates of extinction/persistence and colonisation/failure were put together as binary response variables in separate analysis of extinction and colonisation, respectively. They were analysed using generalised linear models (GLMs) with logit-links and binomial error structures, which are appropriate for binary responses. As explanatory variables the species' traits and environmental factors described above were used, and also the specified interaction terms considered important on an a priori basis (Table 6.4).

Table 6.4. Species traits and environmental variables used in the analysis (see main text for details). Connecting lines show the potential trait-environmental interactions considered.

Species trait	Change in environment	Reference
Average body weight		
Average number of broods		Jiguet et al. (2007)
Average laying date	Change in temperature	Visser et al. (2009)
Average laying period		Crick (2004), Both et al.(2009), Moussus et al. (2010)
Migration behaviour		Both et al. (2009)
Diet group		Both et al. (2009), Moussus et al. (2010)
Habitat preference	Change in predator no	Hromada et al. (2002)

Interactions that have been identified to have significant impacts on population trends (i.e. brood number) were included as well as changes in climatic variables that may affect the impacts of traits (i.e. warmer February temperature may be indicators of extended breeding periods which in turn may increase the number of broods a species is able to lay in a year).

Differences in migration strategy have also been widely associated with variability in climate change adaptation with long distance migrant species being more sensitive to changes in climate as they are less able to adapt to advances in food peaks due to increased temperatures in their breeding grounds (Jiguet et al. 2007, 2009; Both et al. 2009; Moussus et al., 2010).

With regards to diet type, species with more specialist diet requirements and particularly those that rely on highly seasonal food supplies (i.e. insectivorous species) will be expected to be more sensitive to changes in climate as compare to species with more generalist requirements or those that rely on food items with a more constant supply.

Finally, as predator numbers increase the impacts of their predation on species using more exposed habitats may be higher (Whittingham & Evans, 2004).

To reduce the uncertainty in GLM variable selection, Bayesian Model Averaging (BMA) was applied (Raftery, 1995), as implemented in the BMA package (Raftery et al., 2010). Rather than try to identify a single best model, BMA averages over a set of well-fitting competing alternatives, weighted by their posterior probabilities of being the best fitting of the set. The 'leaps and bounds' algorithm was used to efficiently identify up to 1000 good models per number of predictors (Raftery, 1995). These were fitted and then further reduced to a set of well-fitting models by the Occam's window method, whereby models 20 times

less likely than the best-supported model were discarded (Madigan & Raftery 1994). All models in the well-fitting set have Bayesian Information Criteria (BIC) values within 6 units of one another.

The GLM analysis assumes that each species-square combination represent an independent data point. This may be violated by spatial or phylogenetic non-independence of extinction or colonisation rates, species' traits or environmental gradients. We evaluated this by testing for spatial and phylogenetic autocorrelation in the model residuals. Residuals were obtained from each model in the BMA set and averaged, weighed by model posterior probabilities. To assess spatial autocorrelation, we took the mean residual for each grid square across species and calculated Moran's I autocorrelation coefficients among pairs of squares grouped in 10 km distance bins. Likewise, phylogenetic autocorrelation was assessed by taking the mean residual for each species across squares and calculating Moran's I for pairs of species in discrete phylogenetic bins. Phylogenetic distance was extracted from the British Bird phylogeny of Thomas (1991). Phylogenetic distance was in the range 0 from 2, so we grouped species in 0.02 unit distance bins. In both cases, 1000 randomisations of the residuals were used to assess significance. This test for autocorrelation among species and grid squares.

We also calculated the correspondent mixed effect models (with random site and random species) of the final best-supported models to verify that neither sites nor species were producing a bias in the model outcomes.

6.3 Results

The BMA set (GLMs with BIC within 6 units of the best model) for probability of colonisation events contained 4 models and that for extinction 7 (Table 6.4). Both analyses had quite low model-average R^2, as is expected for analyses of binary data (Cox, 1970), but good discriminatory ability (high AUC score), and

were well calibrated (small unreliability index) (Table 6.4). Observed and predicted extinction and colonisation rates at species level were strongly correlated (Fig 6.1a, Fig 6.2a) showing that the models explained substantial proportions of the interspecific variation in extinction and colonisation events, although at the grid squares level these correlations were much lower (Fig 6.1b, Fig 6.2b) indicating that models may explain a significantly lower proportions of spatial variation in species turnover.

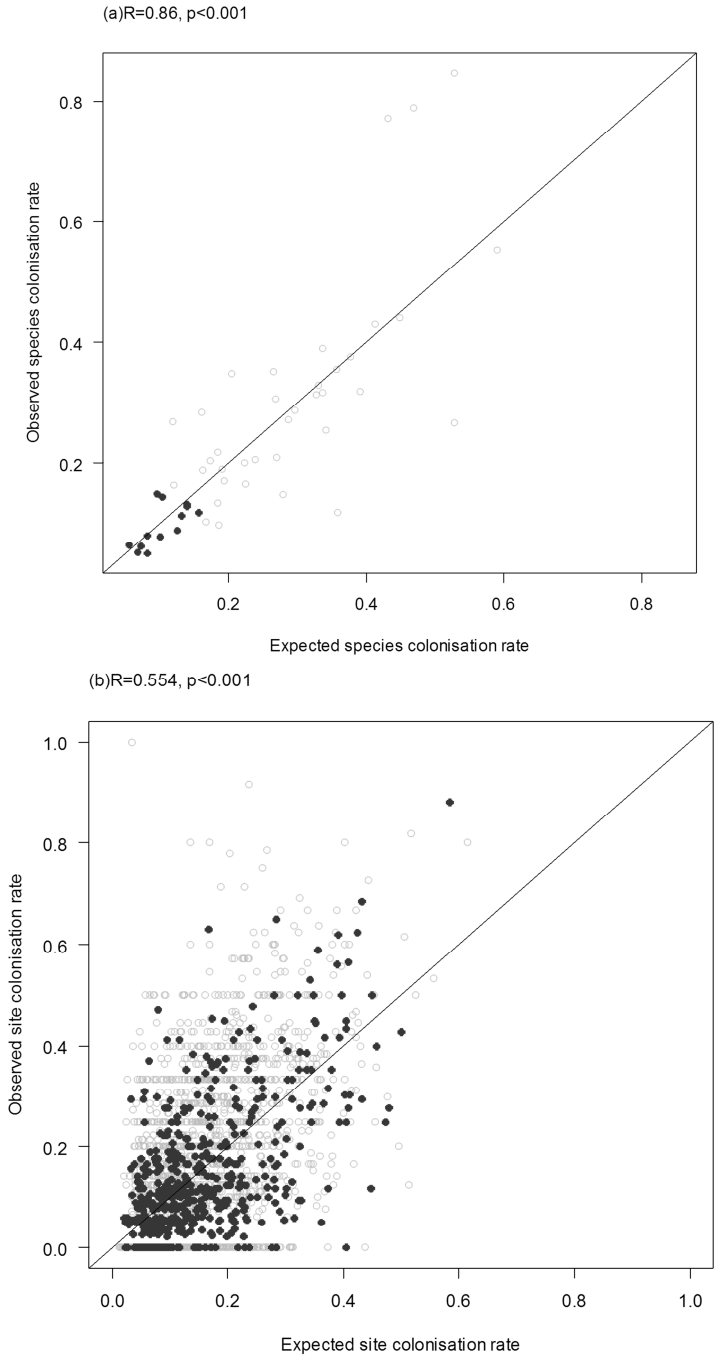


Figure 6.1. Goodness-of-fit plot for the colonisation models of UK passerines. Expected rates for individual species and grid squares were calculated from the means of the model-averaged fitted probabilities (Cox, 1970). Point symbols indicate the number of observations for calculating rates, and hence their accuracy (open grey=lower 50th percentile, filled black=upper 75th percentile). Reported correlations between observed and expected rates are weighted by the number of data points used to calculate the rates. One-sided P-values were estimated from the distribution of weighted correlation coefficients for rates calculated from 1000 randomisations of the fitted probabilities.

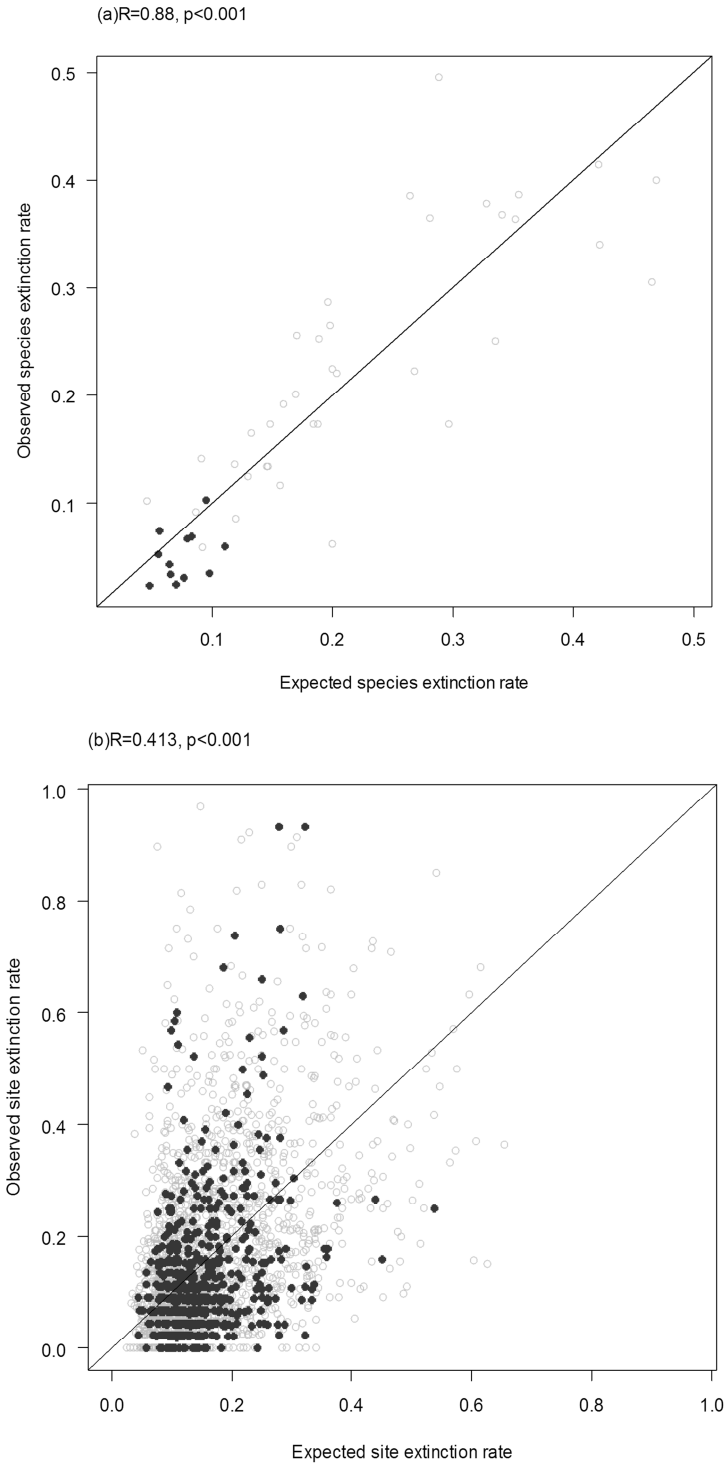


Figure 6.2. Goodness-of-fit plot for the extinction models of UK passerines. Expected rates for individual species and grid squares were calculated from the means of the model-averaged fitted probabilities (Cox, 1970). Point symbols indicate the number of observations for calculating rates, and hence their accuracy (open grey=lower 50th percentile, filled black=upper 75th percentile). Reported correlations between observed and expected rates are weighted by the number of data points used to calculate the rates. One-sided P-values were estimated from the distribution of weighted correlation coefficients for rates calculated from 1000 randomisations of the fitted probabilities.

The top models in both analyses had high posterior probabilities as compared to the subsequent selected models and the relative importance of the predictors retained in final models was high (most of them appearing in 100% of the BMA subset models, see Appendix, supplement C). The only significant traits not present in the final models were woodland species and average laying date in the colonisation model (Table 6.5). Finally, several interactions between species' traits and environmental pressures were identified as significantly contributing to model fit and were consistent with our a priori expectations (Table 6.5).

Both species with larger body masses and productivity presented higher extinction rates and lower colonisation rates (Table 6.5). Also the 1990 prevalence index appears to indicate that species with higher prevalence were likely to have higher colonisation rates and lower extinction rates than species with lower prevalence as expected considering the bias produced by this variable. In terms of resource use, farmland dependent species were less likely to colonize and more prone to extinction than non-farmland species (Table 6.5, Figs 6.3c, 6.4c) and the same is true for woodland species (Fig 6.4d). Regarding migratory behaviour, residents are more likely to colonise than either partial migrants or migrants and the vice versa is true in the case of extinction (Figs 6.3a, 6.4a). In terms of diet groups there are no major differences in terms of extinction though insectivorous species appear slightly more likely to colonize than either generalist or seed eaters (Figs 6.4b, 6.3b respectively). Finally, in terms of brood per year, single brooded species appear less likely to colonize and more likely to go extinct as compared to multiple brooded species (Table 6.3).

In terms of interaction between traits and environmental factors, with regards to diet preferences, while seed-eaters and generalist species were more likely to colonise locations with warming February temperatures, insectivorous kept quite low and constant colonisation rates despite the observed changes in temperature (Fig 6.5a). With regards to extinction rates all groups appear to

have reduced extinction probabilities in locations with warmer absolute temperatures in February, however insectivorous species were slightly more likely to suffer from extinction than either generalist or seed-eaters in these areas (Fig 6.6a).

Both migrants and partial migrant were more likely to colonise warming areas and areas with warmer absolute February temperatures while this was not the case for resident species (Fig. 6.5b). Migrants and partial migrants had reduced extinction rates in locations with warming February temperatures, whereas residents were more likely to suffer from higher extinction rates in these areas (Fig 6.6b). . Also, species laying their eggs earlier in the year were more likely to colonise in warming areas as compare to later laying species (Fig 6.5e). In terms of laying periods species with longer periods had higher extinction rates in areas with colder absolute February temperatures and in those with warming February temperatures (Figs 6.6e,f) while they had increasing colonisation rates in areas with warmer absolute February temperatures (Fig 6.5f).

Single brooded species tend to present increasing rates of extinction in warming areas though species with more broods/year have slightly lower extinction rates (Fig 6.5c). Similar trends are observed in colonisation rates, with increasing colonisation rates in warming areas and particularly so for multi-brooded species (Fig 6.6d). Finally, extinction rates of woodland species decline as the number of predators increases (Fig 6.6c).

Table 6.5. Analysis of colonisation and extinction in UK passerine birds by Bayesian model averaging of generalised linear models (BMA). Model diagnostics include the area under the receiver operating characteristics curve (AUC) and the calibration unreliability index U (testing the null hypothesis that observed and predicted probabilities have a 1:1 correspondence) (Cox, 1970).

Model diagnostics	**Model colonisation**	P	**model extinction**	P
No. data points	28782		88868	
No. models in BMA dataset	4		7	
Posterior probability of best model	0.687		0.401	
R^2	0.349		0.257	
AUC	0.849		0.797	
Unreliability index U (p-value)	$6.9\ 10^{-5}$	0.999	-2.2^{-5}	0.998
Trait effects	Coefficient (SD)	P	Coefficient (SD)	P
Average body weight	-0.001(0)	***	0.0003(0)	***
Average brood/year	-0.58(0.094)	***	0.25(0.036)	***
Average laying date	-		0.013 (0.001)	***
Average 1st clutch laying period	0.009(0.002)	***	-0.007(0.001)	***
Migrant strategy.partial migrant	-0.213(0.11)	.	-0.122(0.042)	**
Migrant strategy. Migrant	-1.018(0.092)	***	-0.244(0.044)	***
Farmland species	-0.492(0.062)	***	0.414(0.034)	***
Woodland species	-		0.328(0.034)	***
diet.seed eater	-0.075(0.121)		-0.022(0.04)	
diet.insect-invertebrate	0.341(0.097)	***	0.05(0.035)	
prevalence90	0.0002(0)	***	-0.001(0)	***
Environmental effects				
Feb_minT2	0.015(0.05)		-0.207(0.034)	***
Change in Feb_minT	0.858(0.36)	*	0.073(0.12)	
Change in predator number	0.297(0.014)	***	-0.366(0.011)	***
Lambda_pt15	1.977(0.035)	***	-1.571(0.024)	***
Trait-environment effects				
Seed eaters*Feb_minT	-		0.007(0.031)	
Insectivorous*Feb_minT	-		0.115(0.024)	***
Seed eaters*Change in FebminT	0.259(0.241)		-	
Insectivorous*Change in FebminT	-0.788(0.178)	***	-	
Woodland species*changepred	-		-0.065(0.016)	***
Partial migrant*Feb_minT	0.006(0.046)		-	
Migrant*Feb_minT	0.089(0.035)	*	-	
Partial migrant*Change in FebminT	1.609(0.223)	***	-0.629(0.09)	***
Migrant*Change in FebminT	2.384(0.197)	***	-0.547(0.069)	***
Average laying date*Change in FebminT	-0.019(0.003)	***	0.005(0.003)	
Average 1st clutch laying period*Feb_minT	0.004(0.001)	***	-0.003(0.001)	***
Average 1st clutch laying period*Change in FebminT	-		0.015(0.002)	***
Average Brood/year*Change in FebminT	0.748(0.164)	***	-0.429(0.079)	***

Significance codes: *(<0.001); **(<0.01); * (<0.05); . (<0.1)**

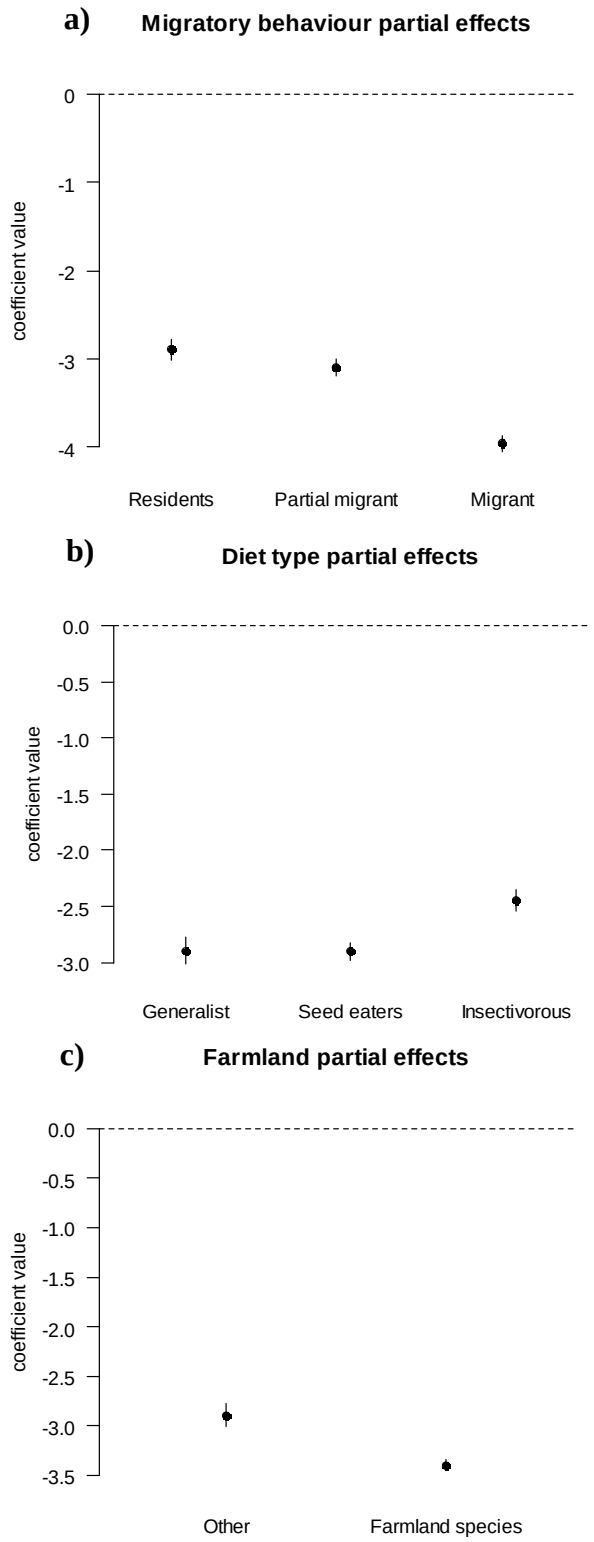


Figure 6.3 Independent effects of species traits on colonisation of UK passerines over the two atlas periods in relation to: a) migration, b) diet type and c) farmland habitat.

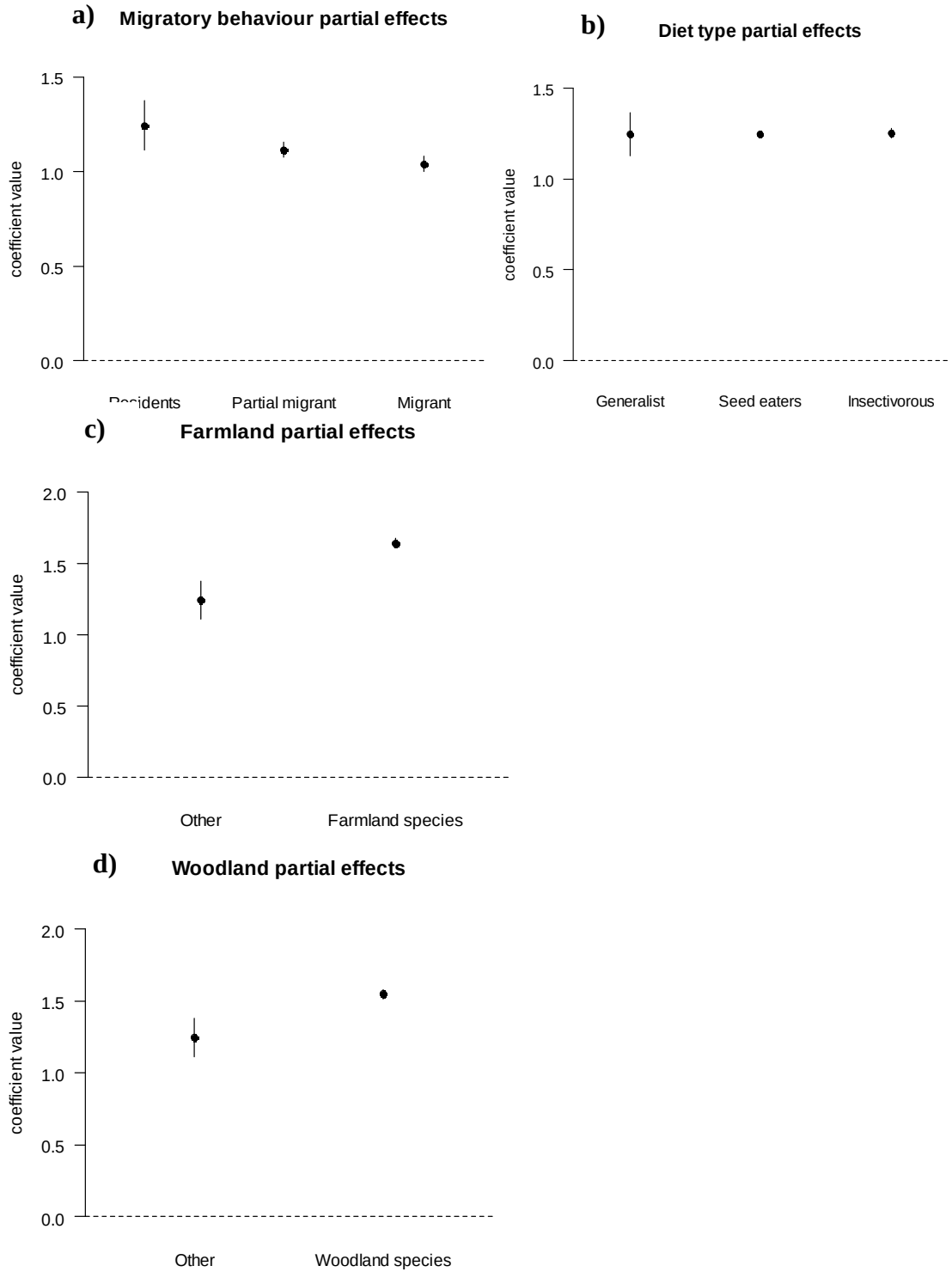


Figure 6.4 Independent effects of species traits on extinction of UK passerines over the two atlas periods in relation to: a) migration, b) diet type, c) farmland habitat and d) woodland habitat.

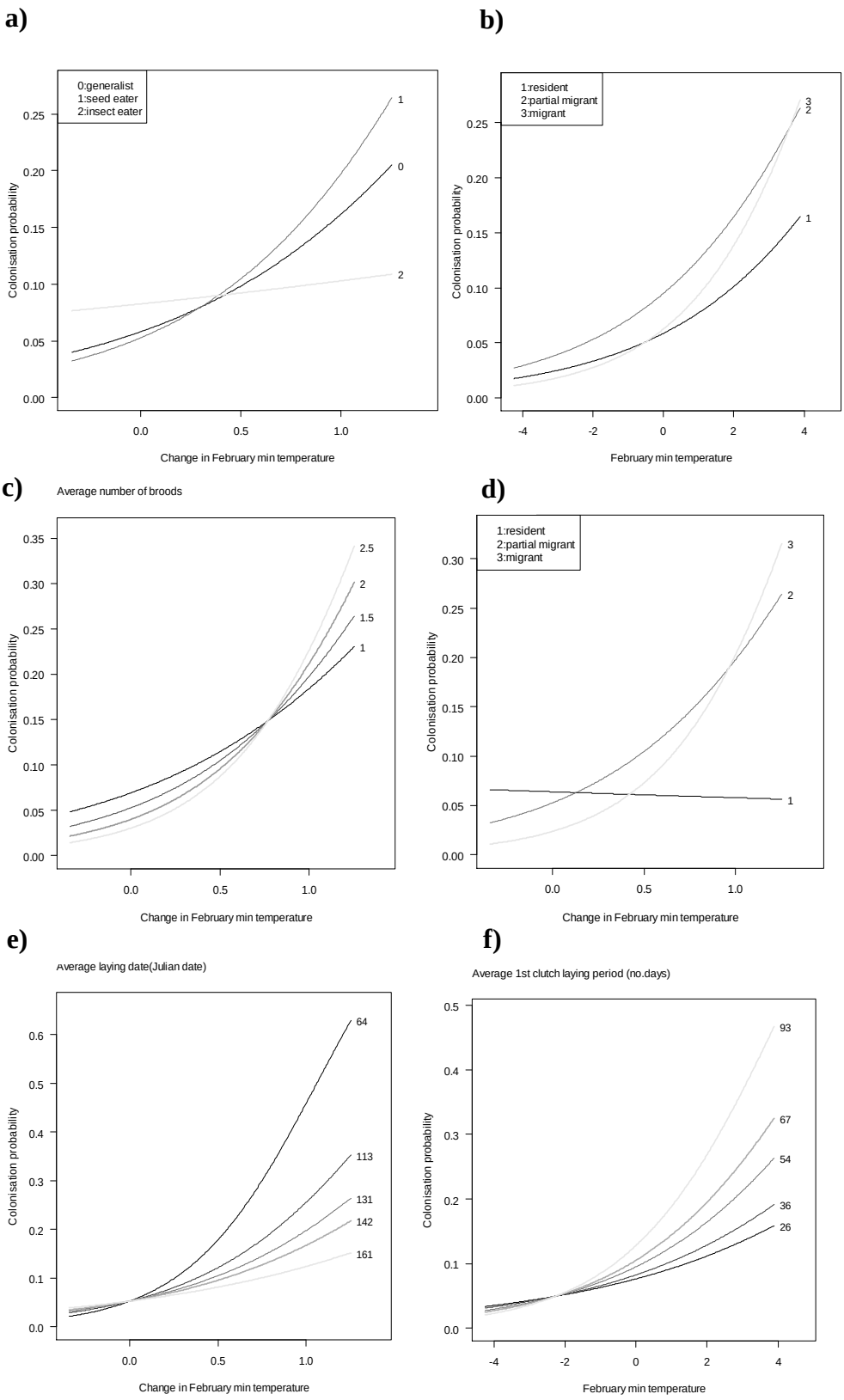


Figure 6.5 Modelled interactions between species traits and environmental pressures that influence colonisation of UK passerines over the two atlas periods

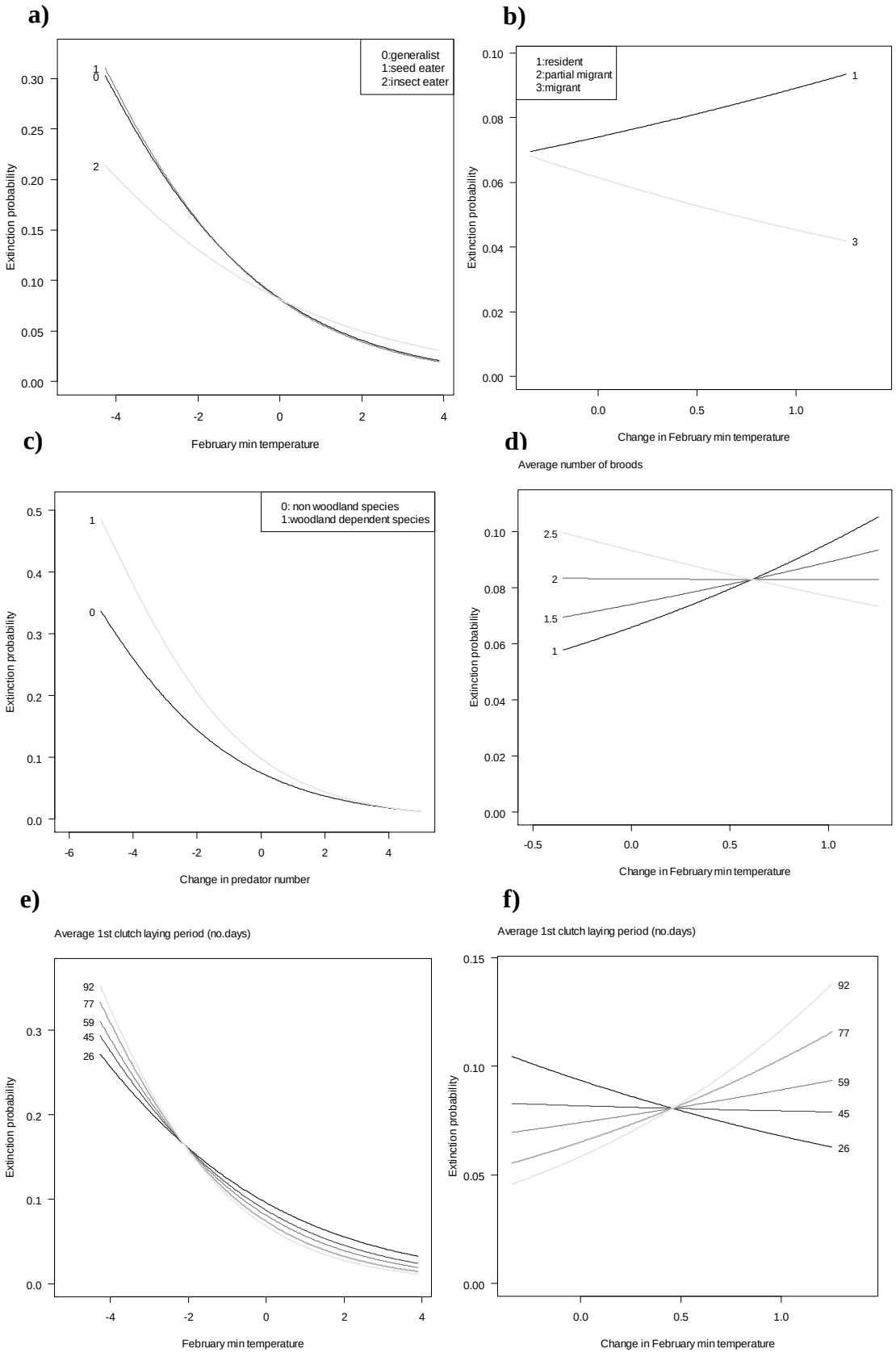


Figure 6.6 Modelled interactions between species traits and environmental pressures that influence extinction of UK passerines over the two atlas periods

6.4 Discussion

6.4.1.Colonisation and extinction dynamics and density of surrounding occupied cells

As expected lambda, or likelihood of adjacent occupied cells, was the most important variable for both colonisation and extinction process. A higher density of surrounding occupied cells favours colonisation processes and reduces the likelihood of local extinction. This highlights the importance of understanding the spatial structure of the species distribution, as it has a key role in the likelihood of a species to colonise or go extinct in a particular place. Species where occupied cells are closer together, or at high local density, within a 30km radius of a focal cell, are more likely to colonise new cells and less likely to undergo local extinction, while the opposite holds for species with more patchy isolated distributions. This is consistent with predictions derived from metapopulation and source-sink dynamics (Levins 1970; Pullian, 1988).

According to these theories, populations exist within a network of patches in which local extinction and colonisation processes take place. However, it has been recognised that the probability of extinction or colonisation of a species not only depends on what happens within individual patches but also on the characteristics of the surrounding matrix of sites (Paradis et al. 2000; Baillie et al, 2002). As Baillie et al., (2002) presented, individuals can move through the landscape until they find a suitable area to occupy, moving up to a maximum number of habitat units after which they will be considered to have gone extinct. In our study this appears to be the case, where colonisation processes are more likely to happen when species find suitable habitats within a buffer area that allows for other surrounding patches to provide sufficient immigration to guarantee the establishment of that species in the new patch. In the case of extinction, more isolated far-away patches seem to suffer from higher extinction rates due to lack of either suitable habitat or sufficient influx of individuals to secure establishment as it has been proposed before (Doxford & Frekleton, 2012).

6.4.2.Environmental pressures and species traits interactions

These analyses highlight the importance of interactions between species traits and environmental factors. Migratory behaviour appears fundamental in a species potential to colonise or go extinct particularly in relation to relative changes in winter temperatures over the study period. Although there is already substantial evidence of the effects of climate change in species (Walther et al., 2002; Parmesan & Yohe, 2003; Crick, 2004) our analysis allows for a direct connection between the role of species traits and concurrent climate change.

Changes in temperature have little impact on colonisation rates in resident species (only slightly reduced colonisation rates with warming climate), partial migrants and migrant species are much more likely to colonise areas with warming temperature than those with little temperature change. With extinction processes, the opposite holds, with partial migrant and migrant species presenting significantly lower extinction rates than resident species in warming areas. This pattern matches the finding reported by other studies carried out on island avifauna (Foufopoulos & Mayer, 2007). The main explanation for these results can be found in the high dispersal ability of, especially, migrant and partial migrant species. This ability to move will allow species to colonise new areas with a climate more suitable to their requirements (colder areas that were previously unsuitable and currently have suffered an increase in temperature that have made them suitable). The contrary would be true for resident species. This could also be related back to the metapopulation dynamics with migrant and partial migrant populations being more likely to rescue populations that may be in trouble as compared to resident species due to their enhance dispersal abilities (Foufopoulos & Mayer, 2007).

Other important interactions for both colonisation and extinction processes are also related to phenological traits and changes in climate but the traits involved in each process are different. While in the case of colonisation average laying date seems to be most important, with earlier laying species presenting larger colonisation rates in warming areas as compared to later laying species, in the

case of extinction it is the length of the laying period that seems to have a major impact in the rates of extinction (with species with shorter laying periods doing better in warming conditions than species with larger ones and vice versa in cooling areas). Temperature may affect laying dates in different ways. It can act as a cue that predicts the forthcoming favourable conditions or can play also a direct role at the time of egg formation (associated with both the development of reproductive organs and production of eggs) (Visser et al., 2009).

In the case of colonisation and laying date, it has already been reported that avian reproduction in the wild is correlated with temperature (Dunn, 2004) with warmer years presenting mean laying dates earlier than cold years. This may also help explain why the same pattern is observed with species with earlier dates being better able to colonise warming areas. Exactly how temperature affects laying date in a mechanistic way is largely unknown (Visser et al. 2009). However, it could be that a potential for more flexible laying periods could confer species with more plasticity in areas where laying may be delayed. Results from previous studies indicate that the period in which temperature plays a role as a cue is late in the cascade of physiological events leading to laying the first egg (Meijer & Drent, 1999; Wingfield & Kenagy 1991). Many field studies have demonstrated a correlation with temperatures experienced weeks before laying but again not just fixed temperatures are important but their relative change will also have a significant role (Visser et al., 2009).

Diet also appears to play a role in the ability of species to colonise or go extinct in relation to winter temperature. However, while for colonisation processes what matters is the relative change in temperature for extinction processes is more related to the absolute temperature. For generalist and seed eating species both colonisation and extinction rates are higher than for insectivorous species in warming areas. This can be due to the difficulties this species might experience in adapting to changes in the period of their prey peaks. For example, as it has already been reported (Perrins 1991) great tits can shift their laying dates in response to earlier warm spring weather but cannot decrease

their incubation period to match that of their caterpillar prey producing a mist-matching event that leads to an early shortage of the prey when their young are more vulnerable.

The importance of brood size in extinction may also be important with single-brooded species more likely to go extinct in warming areas than multiple brooded species which may indicate that facultative multibrooded species may be more able to adapt to conditions (particularly warming climates) than single brooded.

6.4.3.Colonisation and extinction dynamics and independent effects of environmental pressures and species traits

In terms of independent effects, in both processes migratory behaviour appears to have a major role in the potential of species to colonise or go extinct. In colonisation processes the dependency of species to particular habitat (farmland) has a noteworthy detrimental effect on the potential of species to colonise new habitat and the same dependency (farmland or woodland) deems species more likely to suffer extinction processes. Also increasing body size appears to have a detrimental effect of species with less likelihood to colonise and more changes to go extinct. This pattern has been reported to bird species before (Gaston, 2006; Patten &Smith-Patten 2011) though the mechanisms by which this affects colonisation or extinction processes is not yet clear. Body mass is correlated in a complex manner to a variety of other life-history traits and can affect species dispersal, establishment and persistence in a variety of direct and indirect ways (Gaston and Blackburn, 2002; Pimm et al., 1988; Foufopoulos & Mayer, 2007).

With regards to the impact of independent environmental factors, apart from the already mentioned effect of climate, the number of predators present also appeared as a top driver of both colonisation and extinction processes with more colonisation and less extinction occurring in more predator dense areas.

This goes against our initial expectation but could be indirectly link to other environmental variables not included on the study such as use of pesticides or habitat quality.

In order to protect biodiversity species under threat have to be described and the main environmental pressures identified in order to be able to propose adequate measures of conservation (Purvis et al., 2000). This study has provided an approach in which species characteristics and environmental drivers can be analysed simultaneously and provides direct information on the interactions between the main pressures and species characteristics that may be driving colonisation and extinction dynamics in UK passerines at broad scales. The key role of phenological traits (including migratory behaviour) in driving the responses of species to climate change in terms of colonisation and extinction processes highlights the importance of these variables in conferring species resilience to environmental pressures. As new indicators are being developed to monitor and track the status of species and general biodiversity (i.e. IUCN Red Lists, UK conservation status categories), it may be of interest to take into account measures of vulnerability and/or resilience related to species ability to withstand climatic change.

Chapter 7 : General Discussion

Environmental change presents the greatest challenges to biodiversity conservation. From climate change to land cover conversion and pollution effects, global biodiversity faces many threats. Though conservation actions have been put into place to halt the loss of biodiversity, a recent review suggests that conservation actions have largely failed to do this (Bradshaw, 2010). Hence, understanding the links between species responses, environmental pressures and the role of species characteristics in conferring resilience to these environmental changes is fundamental for developing adequate conservation measures.

This thesis focuses on a range of approaches to investigate the impacts of well-known environmental pressures on the avian community in the UK, with a particular interest on passerines, to try to uncover mechanisms underpinning species responses to environmental change. Furthermore, considering that bird species are already used in a variety of indices currently applied as biodiversity indicators (e.g. Gregory & van Strien, 2010), it would be of great value to identify new avenues to measure and monitor species responses to environmental change that would help improve the current set of indicators.

In order to do this, this thesis had a number of aims to establish and further analyse the relationship between population trends and species characteristics in the UK. My aims were to:

1. Identify the impacts and contribution of the main environmental pressures on the UK avian community [Chapters 3 and 4].
2. Assess how these impacts may have changed over time [Chapters 3 and 4].
3. Determine which traits may be associated with model suitability [Chapters 3 and Chapter 5]

4. Determine if niche characteristics show any responses to environmental pressures and if change over time was related to any species traits so that their suitability as monitoring tools could be assessed [Chapter 5].
5. Establish if there are particular environmental pressures and species traits driving colonisation and extinction processes in this study group which could be incorporated into current measures of extinction risk [Chapter 6].

Specifically the following questions were addressed:

- Are passerine species with particular ecological or life history characteristics more vulnerable to population declines? [Chapter 2]
- Are observed population trends influenced by species phylogenetic history? [Chapter 2]
- What is the relative importance of climate, land use, pollution and biological factors as drivers of current avian assemblage patterns in the UK? [Chapter 3]
- What are the major changes observed in the relative importance of key environmental driver over time on the UK passerine community? [Chapter 4]
- How do species characteristics relate to community model performance? [Chapter 4]
- What are the main external factors driving changes in species' niche characteristics? [Chapter 5]
- Which species traits are associated with ability to track environmental changes? [Chapter 5]
- How do niche characteristics relate to species current conservation status? [Chapter 5]
- What are the key environmental drivers and species characteristics operating colonisation and extinction dynamics in the UK? [Chapter 6]

- Are there any particular interactions between traits and drivers that produce particular colonisation or extinction patterns in species? [Chapter 6]

7.1 Main findings and novelties of this thesis

As there is substantial inter-specific variation observed in the magnitude and direction of responses to environmental change, identifying the mechanisms underlying species' responses is essential for developing adequate conservation strategies for the most vulnerable species (Jiguet et al., 2009; Végvári et al., 2009). Throughout this thesis, ecological responses have been linked to species' ecological traits with the aim of gaining a greater understanding of the mechanisms underpinning species' differential responses to environmental change and identifying those trait groups that may be most vulnerable or most valuable as indicators.

Chapter 2 constitutes one of the first attempts to relate population trends to the full range of resource use, life-history and phenological traits within the same analytical framework in contrast to many previous studies which have focussed on only one or two of these major trait groups (e.g. Moller et al. 2008, Jiguet et al.,2009; Van Turnout et al., 2010; Thaxter et al., 2010; Ockendon et al., 2012).

This approach was valuable in revealing key ecological characteristics, namely wide resource use and phenological flexibility, traits that buffer species which possess them against environmental change, but it also highlighted the interaction between traits in governing species responses to change. The ability to shift phenology patterns was particularly critical to migrant species (i.e. migrants with longer laying periods and advanced arrival dates were less likely to have declining populations). This finding is mirrored by other studies relating population trends to multiple ecological traits (Van Turnhout et al. 2010) and has implications for improving the design of future wild bird indicators which

should take into account these trait interactions and their effect on species responses when establishing new indicator categories.

This study also reiterates previous findings that farmland species in the UK are more vulnerable to population declines and reinforces the value of this habitat-based indicator. This finding has been attributed to a range of processes resulting from agricultural intensification, namely loss of hedgerows, increasing use of chemical products (fertilizers and pesticides) and changes in crop and ploughing systems. These all have negative impacts on survival and fitness of farmland species during the wintering period, and in turn influence species pre-breeding conditions (Chamberlain et al., 2000; Gregory et al., 2005; Wilson et al., 2009).

Species-specific traits may result in complex and potentially opposing responses to environmental conditions across the annual cycle, which need to be understood fully in order to be able to determine their ultimate effect on population trends (Jenni & Kéry, 2003). This is essential, given the widespread finding that taxa across terrestrial and aquatic environments are shifting their phenology but are becoming increasingly poorly-matched to the key resources on which they depend (Thackeray et al 2010). Trophic interactions should, therefore, be considered when linking species traits to population trends or other ecological responses. This has largely been possible only where lower trophic levels are included in long-term monitoring or systematic surveys (Burthe et al. 2012). Overall, trait-based forecasts of species population trends or range changes face large challenges of quantifying relevant variation in traits across and within large number of species and being able to couple these data with both abiotic and biotic extrinsic factors (Angert et al. 2011).

Therefore, taking advantage of recent advances in spatial data and ecosystems modelling for the UK, in Chapters 3 and 4 I examined the role of multiple environmental pressures in determining avian community composition in the UK, and how the importance of these pressures may have changed in recent

decades for passerine communities in particular. Firstly, examining multiple pressures within the same framework demonstrated that land cover and pollution drivers are of equivalent importance to climate in structuring bird communities at the broad-scale in the UK. Secondly, investigating the impacts of geographic variables, namely temperature regimes between seasons that directly corresponded to critical annual events in passerine life cycles, rather than simply focussing on annual mean temperatures, revealed winter conditions to be key in structuring passerine communities.

Though the community approach adopted here demonstrated that birds and passerines in particular are responsive to multiple environmental pressures, these pressures are spatially-structured and interact strongly at the scale of this study (10km). For design of mitigation strategies, it is better to be able to quantify the precise impacts of individual pressures in particular contexts and on particular functional groups; for example, coastal species and raptors were found to respond differently to other groups to pressures such as climate and land use and the accuracy of community models at reproducing particular species distributions depended on traits. For example, the efficacy of the community models to explain the observed variance in passerines depended on the level of specialisation of the species with habitat constrained species such as woodland and wetland species being better modelled than more generalist or highly specialized species. This will indicate that these community models could be used also as tools to measure habitat quality.

New statistical and ecological frameworks are being developed to address this need to disentangle multiple stressors (Ormerod et al. 2010). These range from simple path analyses for teasing apart the relative contribution of related stressors (e.g topographic heterogeneity, altitude and climate in mountain environments – Ruggiero & Hawkins 2008) to complex ecosystem models (Haines-Young & Potschin, 2010). The latter explicitly represent drivers (e.g. intense land use) that cause pressures (e.g. eutrophication) and consequently ecosystem state (e.g. ecological status). This has impacts on ecological status

or ecosystem service capacity, which requires a management or policy response (e.g. restoration work). Due to the high quality of distribution and population data, terrestrial avian biodiversity is starting to be incorporated into such ecosystem service models (Anderson et al. 2009; Holland et al. 2011).

Multivariate ordination techniques were also used; these methods are designed to investigate species-environment relationships and provide an overview of the species assemblages (Doledec *et al.*, 2000). Chapter 5 used this approach to model niche parameters and dynamics in UK passerines and to relate niche dynamics to species traits. This chapter constitutes one of the first comparative studies that evaluate niche evolution and characteristics in relation to species traits within a single taxonomical clade. The analyses were designed to determine the relationship between the differential responses of target species in terms of the niche characteristics and changes in environmental pressures.

The first important result was that some species changed their position significantly in ordination space between the two time periods indicating evidence for niche tracking in a community setting, supporting Tingley *et al*. (2007) who demonstrated that species niches tracked changes in temperature and precipitation. Species also tended to change their niche properties in response to local environmental changes. This chapter indicated that both niche tracking and niche dynamics are important processes in the community dynamics of UK passerine species. As has been argued before (DeVictor et al. 2009, Tingley et al, 2007), niche dynamics should be incorporated and taken into account when developing predictive models aimed at informing conservation efforts towards threatened species.

Finally, a key goal for conservation is mitigating the extinction risk for vulnerable species. Understanding how species traits impact on species responses to environmental change is fundamental to this process. A burgeoning literature has established relationships between species traits and extinction risk. For

example, large body size, long generation time and ecological specialisation are associated with IUCN red list measures of vulnerability (Purvis et al 2005).

Rather than using global indicators, Chapter 6 modelled extinction and colonisation processes at a regional scale. These analyses demonstrated the role of both environmental and species specific factors in determining both colonisation and extinction processes as well as providing direct evidence for the divergence in species responses to changes in environment according to particular traits. Unsurprisingly, spatial structure strongly predicts colonisation and extinction: cells near others that are currently occupied were more likely to be colonised and less likely to have an extinction event.

Additionally, a number of species traits, including migratory behaviour and phenology, were shown to interact with environmental changes to predict extinction and colonisation probabilities. For example, warming temperatures were associated with increased colonisation for migrants. Species with more annual broods were less likely to show extinction in cells with temperature increase. Average laying date seems to be most important for colonisation while early-laying species had higher colonisation rates in warming areas as compared to later laying species.

Extinction was most strongly predicted by the length of the laying period (with species with shorter laying periods doing better in warming conditions than species with longer laying periods and vice versa in cooling areas). The consistent relationships between temperature change, laying phenology and extinction are likely to be the result of a cascade of physiological events leading to laying the first egg (Meijer & Drent, 1999; Wingfield & Kenagy 1991). Ecological specialisation rendered species less likely to colonise new cells more likely to go extinct. This has been demonstrated elsewhere with bird species with greater potential for ecological generalization, namely broader habitat and diet niches presenting greater establishment success (Vall-Llosera & Sol, 2009)

In general, it seems that the most consistent traits conferring resilience to environmental change across all analysis (being species population trends, niche parameters or colonisation/extinction rates) are phenological characteristics (i.e. flexibility in laying or clutching periods) and particularly for species that will otherwise be significantly vulnerable (i.e. migrants). This significant effect of climate on broad range of species parameters confirms its dominance at this regional/landscape scale. This not only highlights the importance of climate change in driving environmental change and consequently species responses but also heightens the relevance of particular groups as indicators and tools to develop adequate adaptation and mitigation measures. However, is not only phenological traits and climate that seem to be driving species responses to environmental change but also resource use specialization such as farmland species in terms of habitat use and insectivorous species in terms of diet range. These specialized species appear to be more vulnerable to climatic changes in the environment as shown by the colonisation/extinction and niche models where they present higher extinction rates and decrease niche stability as compared to more generalist species which could prove to be useful focus species when trying to develop mitigation strategies for conservation under particular environmental changes such as land use change.

Together, all these analyses and results demonstrate the strong relationship between species traits and environmental change and how their responses are consistently dependent of particular set of traits. Thus, if we really want to tackle species loss and implement more effective bioindicators for adaptive management and conservation these are concepts and information that should be readily incorporated in these indices.

7.2 Contributions of this thesis to knowledge on bioindicators and conservation and suggestions for further research

In general, indicators have been categorized into four classes according to their ability to generate findings and their strength of relationship with environmental factors (Van Strien et al. 2009) (Fig 7.1).

Type 1 indicators will be those that measure how specific species or groups are doing (i.e. species of conservation concern). Type 2 are indicators that are able to represent more general trends observed in other groups within the study area. Type 3 are indicators used to show how specific species or groups are responding to environmental pressures, and finally, Type 4 are those that can show how biodiversity is responding to environmental factors in general.

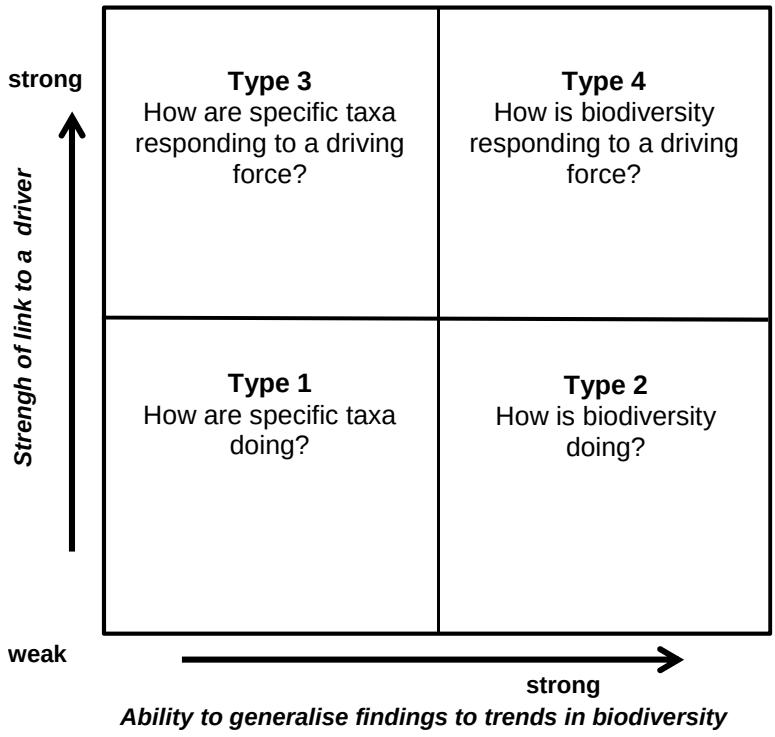


Figure 7.1. Indicator categories based on their relationship to drivers and their ability to represent the overall environment (from Van Strien et al., 2009).

The results and evidence gathered in this thesis indicating that a variety of population and community measures (i.e. community patterns, colonisation and extinction rates, niche area, species marginality) are related not only to one but various environmental pressures (i.e. temperature change, pollution, land cover change) and a range of previous studies supporting similar results (Sparks & Crick, 1999; Thomas & Lennon, 1999; Crick, 2004; Jetz et al., 2007). Hence it would seem that these passerine birds could be considered Type 3 indicators. However, as it has been described, not all species present the same response to the studied environmental pressures, as these are related to a wide range of interacting traits and the scale of action of the characteristic traits as mentioned in the previous section. For example, since migration behaviour, habitat use and phenological flexibility appear to have interactive effects on the ability of species to adapt to environmental change, biodiversity components such as climate change may be better monitored using separate indicators for migrants and resident species.

However, in relation to the woodland wild bird indicators, many of the woodland passerines in the UK may be vulnerable to change due to their migrant status preferred diets (restricted/insectivorous), calling into question the value of habitat-based indicators alone for understanding the mechanisms underpinning population declines. A recent cross-region study pointed out that though trait-based analyses of population trends can reveal strong explanatory relationships within particular regions (species faring badly tended to be medium-sized, had relatively short incubation and fledging periods, were longer distant migrants, had small relative brain sizes and were farmland specialists), these perform poorly when used to predict species vulnerability in other regions (Pocock et al. 2011), and thus, may be valuable mainly for setting local rather than regional or global conservation priorities.

Despite the fact that bird species are considered, in many cases, as adequate surrogates for other biodiversity groups and are used in a number of bioindicator indices, the question still remains if they are truly surrogates of the overall biodiversity. Birds use their environment in a way and at a spatial scale quite different to other taxa (Gregory et al., 2008). They are highly mobile, and a large number of species migrate (integrating a range of environmental pressures that extend over large expands of land) (Gregory et al., 2008). There is little evidence for a correlation between bird numbers and responses and those of other taxa, hence the generalization of their responses their use as tools to quantify the overall state of biodiversity should be done with great caution (Gregory et al., 2008). Hence, it would be of great use if further effort was put into investigating and carrying out similar studies as the one presented in this thesis but for other taxonomic groups for which data could be readily available (i.e. insects, plants). Comparative studies that look at the differential effects of a range of environmental pressures could help determine if indeed bioindicators based on particular bird groups could be effective at monitoring and representing the overall state of the environment.

Throughout this study all three pressures (i.e. climate change, land cover transformation and pollution) appear to have importance at a community level (though with different independent effects) through their impacts are rather different in terms of niche and extinction colonisation dynamics. As expected, it is mainly the broader environmental pressures (i.e. climate and pollution) that seem to be the main forcing agents at this scale. However, it would have been of great interest to investigate if their importance as environmental pressures varied between spatial scales. Taking into consideration that the choice of scale when conducting ecological studies will determine and influence the results and applications that can be demonstrated and applied respectively (Coreau & Martin, 2007), if these models were to be used as conservation tools it would be fundamental to have information on a variety of scales at which the conservation actions could be implemented (Sodhi et al., 2011). Therefore,

future analyses looking at how to best measure environmental change through different bioindicators should be focused at the scales at which the phenomena of interest are dominant (Pearson & Dawson, 2003).

Also by taking a mixed approach looking at the responses of indicator species to current environmental change and the potential environmental change could help in establishing effective adaptation options for the conservation of vulnerable species (Pearce-Higgins et al., 2011). For example, in this study it has been demonstrated that vulnerable species such as migrants have the potential for colonising new areas if habitat conditions are suitable and their phenological traits track climatic change in their environment. Hence these species could serve as indicators of potential range shifts driven by climate change that could help define a network of protected areas where adaptation measurements could be implemented.

7.3 Limitations of this thesis.

Data sets

There is a need to understand how environmental conditions vary in space and time as well as how organisms respond to those conditions in order to comprehend the mechanisms that may be conferring resilience or vulnerability to environmental change to certain species. To do this, data on both the status of environmental drivers and species characteristics is required. This study has examined the relationship between known drivers of UK ecosystems change in relation to bird population trends and distributions.

Data on bird status was obtained from: the Breeding Bird Survey (BBS) and from the two Atlas of Breeding Birds in Britain and Ireland (1988-91 and 1968-72). Both population trends of the BBS and records from the BB Atlas were considered reliable sources as work has been carried out to assess the

precision and reliability of both and to ensure that data are based on reliable data and sufficient sample sizes (Gibbons et al., 1993; Risely, 2009).

Information on species traits was gathered from a number of sources that were not necessarily gathered concurrently with the data on species status. This should not cause any major problems with most species traits, particularly those related to life history traits, however for characteristics that may be influence by temporal variables this should be taken into consideration (i.e. phenological traits). Considering the time constrains and limited material resources the issues with variable mistiming were considered acceptable and kept in mind when interpreting the results. However, it should be noted that, when possible and feasible, changes in population trends ,characteristics species traits (such as phenology, diet, etc…) and environmental data should be taken synchronously to minimize noise and error in the data and ensure that inferences are really due to changes are occurring parallel to each other in both space and time. Despite this asynchrony, the results still suggest that phenological and other

Also data on species and environmental data were gathered from different sources that, though covered the same time periods and regions, were not simultaneously gathered. Data on land cover was obtained from land cover maps available for the 1990 period, though when studying change over time products from the Ecochange project were used. This project used a range of modelling techniques to reconstruct the land cover map for 1960 based on the World Agricultural Atlas (Mucher et al. 2009). As with any interpolation method, certain level of error was expected but since the analysis were looking at broad land cover uses these were deemed acceptable. In a similar manner, data for pollution was obtained from the FRAME project where data for the 1970s period was also calculated through different interpolations methods (Malgorzata et al., 2009). As mentioned before, though the synchrony between species and environmental data is not flawless (particularly for the baseline periods) considering the logistical and material limitations the used data were considered

more than appropriate for the study at hand though ideally concurrent data collected at the same squares during the same time period would be more suitable.

One final point with regards to the data quality used in this study has to do with the evaluation of biological drivers of environmental change. Though I aimed at introducing a measure of biological variables to quantify the role of these drivers in the system, this may have been relatively rough. It has been established that both competition and predation are significant factors operating at local scales in ecosystems (Thaxter et al., 2010; Rojas-Ahumada et al., 2012). In order to present these biotic interactions I included a crude estimate of the number of bird competitor and predator species based on species records on the two atlases. These estimates may not be the most appropriate but still indicated in both the community and colonisation/extinction analysis that are variables to take into consideration when looking at the importance of different environmental drivers. A more refined approach may be possible by introducing population estimates of known predators (both bird and mammals) acquired through concomitant surveys such as the Wider countryside Survey Schemes (Battersby, 2005).

Study Scale

Ecological processes are often simultaneously influenced by factors acting at a range of scales (Cushman & McGarigal, 2002). The relationships between species and environmental pressures may change qualitatively and quantitatively with the scale of observation and at different scales different processes may be driving the observed species patterns (Thrush et al., 2005; Coreau & Martin, 2007). Therefore, taking the spatial scale of the study into consideration is essential when validating models in terms of useful ecological information and ultimately as useful predictive tools for conservation formulation.

In this study, only processes at the spatial scale of 10 km^2 were analysed. This corresponds to the resolution of the species data used (i.e. breeding bird atlas) and can be considered a meso-scale in terms of spatial resolution. While data on a number of environmental pressures was collated (i.e. temperature and precipitation, land cover, pollution and biotic variables such as human and livestock density) and their effects were significant in a variety of species responses (i.e. colonisation and extinction patterns, community patterns and niche structure), this broad-scale may overlook finer-scale relationships. For example, it has been acknowledged that at global and regional scales mainly climate predictors will drive species distributions while at more regional and landscape scales land cover factors may take precedence and biotic interactions will be regulating processes at more local-scales (Fig 4.1) (Coreau & Martin, 2007).

The results of this study are restricted to broad-scale patterns and though they show interesting results they should be used within the constraints of this spatial scale. However, as a suggestion for expanding the scope of this project it would be interesting to investigate the roles of the key environmental pressures at different scales. A multi-scale analysis of the different environmental pressures acting on the avian community will allow for a more detailed picture of which drivers may be acting at different scales and as a result enable development of specific conservation actions for each spatial scale. These will also determine if they matched results outlined by similar studies suggesting differential roles of drivers as one move through the spatial scales (Pearson & Dawson, 2003; Coreau & Martin, 2007; Fletcher & Hutto, 2008).

APPENDIX.

A. Supplementary information to Chapter 2.

Multivariate analysis of diet data

Data on presence or absence of food items in the diet of each species was analysed using hierarchical cluster analysis to group species that shared similar patterns of food used (i.e. diet types) together.

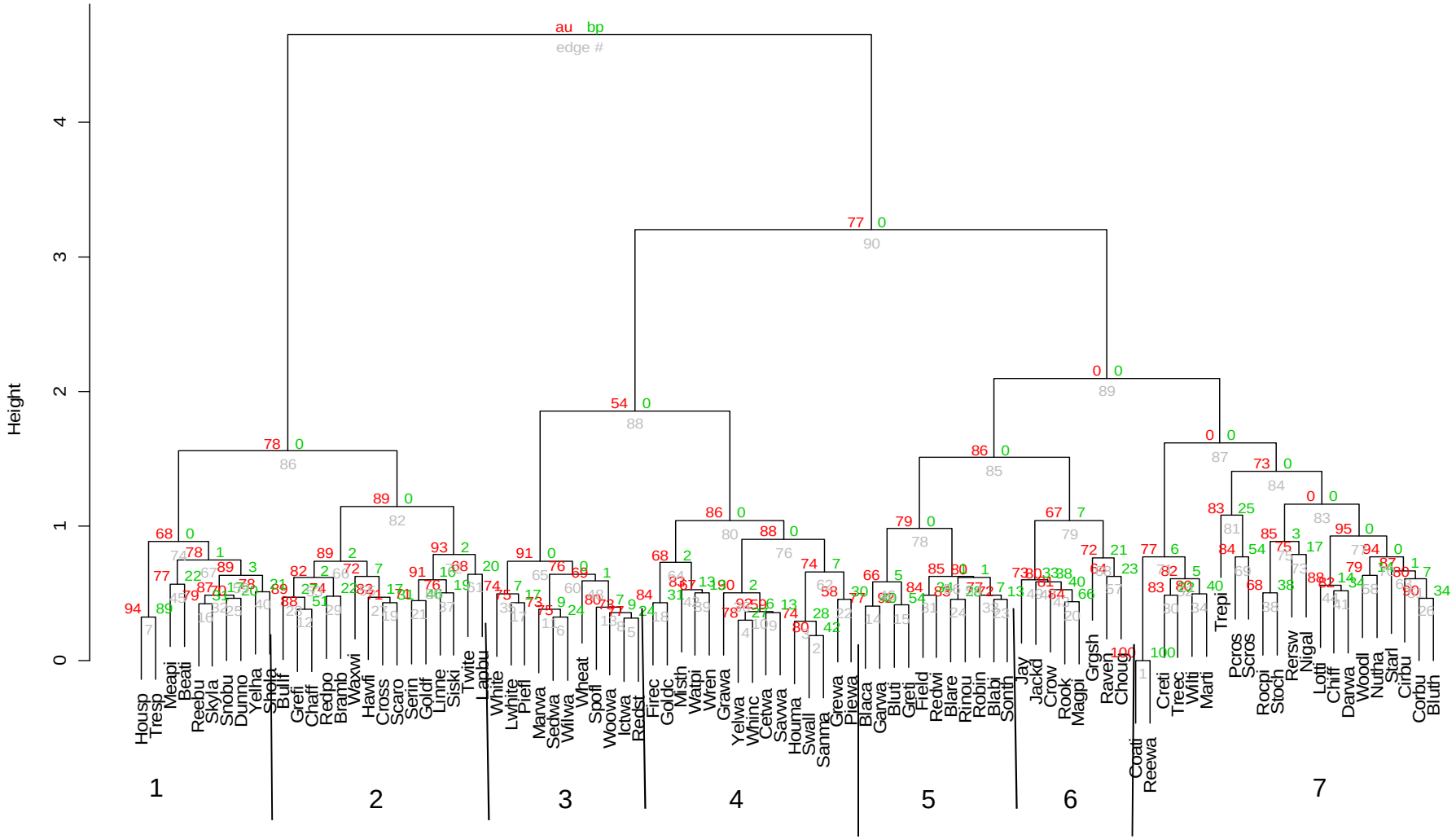
The analysis was run in R using the package *pvclust* (Suzuki &Shimodaira, 2006). This package can be use to assess the uncertainty in hierarchical cluster analysis using approximately unbiased p-values (AU) as well as bootstrap probability values (BP) for each node of the selected optimum tree. In this case, the most parsimoniously tree was obtained with 50,000 bootstrap replications using *binary* as the distance measure and *ward* as the agglomerative method for the hierarchical clustering.

Table A.1. List of species, population growth rates and main trait predictors used in the final analysis

Common Name	Latin name	Instant growth rate	Standard error	Migratory behaviour	Average first clutch laying period (no. days)	Productivity (no.eggs/ year)	Average laying date (Julian date)	Diet group	Habitat	Average body weight (g)	Average Nesting period (no. days)	Nesting location	Mean change in arrival date (no.days)	Mean distance (˚ latitude)
Blackbird	*Turdus merula*	2.116	0.270	Partial migrant	23	10	112	Generalist	Urban	102.5	28.5	vegetation	-	-
Blackcap	*Sylvia atricapilla*	5.159	0.676	Migrant	54	7.125	130	Generalist	Woodland	20	25	vegetation	-0.41	19.63
Blue Tit	*Cyanistes caeruleus*	0.964	0.404	Partial migrant	29	10.5	116	Generalist	Urban	11	33.5	hole	-	-
Bullfinch	*Pyrrhula pyrrhula*	-0.986	0.856	Resident	83	11.875	137	Large seed	Generalist	21	31	vegetation	-	-
Chaffinch	*Fringilla coelebs*	1.157	0.167	Resident	48	4.5	120	Large seed	Generalist	23.5	27	vegetation	-	-
Chiffchaff	*Phylloscopus collybita*	3.159	1.289	Migrant	59	11.5	122	Highly specialist	Woodland	8	28.5	vegetation	-0.39	22.55
Corn Bunting	*Emberiza calandra*	-2.681	0.663	Resident	61	9	167	Highly specialist	Farmland	47	25	ground	-	-
Carrion Crow	*Corvus corone*	1.195	0.374	Resident	46	3.5	97	Generalist, carrion	Urban	510	48.5	vegetation	-	-
Dunnock	*Prunella modularis*	2.129	0.273	Resident	75	10	117	Small seed	Generalist	20.5	28	vegetation	-	-
Garden Warbler	*Sylvia borin*	-1.867	0.544	Migrant	44	4.25	141	Generalist	Woodland	19	24	vegetation	-	-
Goldcrest	*Regulus regulus*	2.357	1.118	Resident	60	19.5	122	Invertebrate	Woodland	5.75	35	vegetation	-	-
Goldfinch	*Carduelis carduelis*	3.393	0.488	Partial migrant	84	12.5	145	Large seed	Farmland	16.5	29.5	vegetation	-	-
Greenfinch	*Carduelis chloris*	3.018	0.476	Resident	91	10	130	Large seed	Urban	27.6	29.5	vegetation	-	-
Great Tit	*Parus major*	3.943	0.324	Resident	37	9	116	Generalist	Generalist	18	33.5	ground	-	-
Grey Wagtail	*Motacilla cinerea*	4.088	2.004	Resident	77	10	117	Invertebrate	Generalist	18	27.5	vegetation	-	-
House Sparrow	*Passer domesticus*	-0.462	0.266	Resident	106	10.625	134	Small seed	Urban	31	30	ground	-	-
Jackdaw	*Corvus monedula*	2.591	0.368	Resident	37	5	89	Generalist, carrion	Generalist	222.5	52.5	hole	-	-
Jay	*Garrulus glandarius*	0.916	0.425	Resident	60	6.25	90	Generalist, carrion	Woodland	166.25	39.5	vegetation	-	-
Lesser Whitethroat	*Sylvia curruca*	-0.570	1.012	Migrant	51	4.75	139	Insect	Woodland	12	24	vegetation	-0.17	27.79
Linnet	*Carduelis cannabina*	-1.690	0.492	Partial migrant	84	7.5	133	Large seed	Farmland	18.75	27	vegetation	-	-
Long-tailed Tit	*Aegithalos caudatus*	0.080	0.613	Resident	36	10.25	98	Highly specialist	Generalist	8.5	33	vegetation	-	-
Magpie	*Pica pica*	-0.264	0.287	Resident	26	6.25	112	Generalist, carrion	Urban	219.5	48.5	vegetation	-	-
Marsh Tit	*Poecile palustris*	-0.702	0.952	Resident	27	8	110	Highly specialist	Woodland	11.5	34.5	vegetation	-	-
Meadow Pipit	*Anthus pratensis*	-1.043	0.390	Partial migrant	59	8	127	Small seed	Upland	18.5	27	ground	-	-
Mistle Thrush	*Turdus viscivorus*	-0.453	0.381	Partial migrant	66	9	97	Invertebrate	Generalist	119	31	vegetation	-	-
Nuthatch	*Sitta europaea*	4.643	0.681	Resident	26	8.75	113	Highly specialist	Woodland	23.5	41	vegetation	-	-
Pied Wagtail	*Motacilla alba*	0.650	0.515	Partial migrant	77	11	137	Invertebrate	Wetland	21	27.5	vegetation	-	-

Raven	*Corvus corax*	8.110	1.547	Resident	45	4.75	64	Generalist, carrion	Upland	1188.75	61.5	vegetation	-	-
Redstart	*Phoenicurus phoenicurus*	-0.404	0.823	Migrant	36	9.375	133	Insect	Woodland	15	30	vegetation	-0.1	33.93
Reed Bunting	*Emberiza schoeniclus*	2.508	0.530	Resident	66	7.5	132	Small seed	Wetland	20.25	26	ground	-	-
Reed Warbler	*Acrocephalus scirpaceus*	2.638	0.581	Migrant	67	6.375	161	Highly specialist	Wetland	13	24.5	vegetation	-0.39	44.6
Robin	*Erithacus rubecula*	1.620	0.464	Partial migrant	83	7.5	108	Generalist	Urban	17.25	29.5	vegetation	-	-
Sedge Warbler	*Acrocephalus schoenobaenus*	0.031	1.358	Migrant	59	5.5	143	Insect	Wetland	12	27.5	vegetation	-0.27	62.1
Skylark	*Alauda arvensis*	-0.900	0.208	Resident	77	12.75	139	Small seed	Farmland	38.25	27	ground	-	-
Song Thrush	*Turdus philomelos*	2.162	0.447	Partial migrant	92	10	111	Generalist	Urban	82.5	29	vegetation	-	-
Spotted Flycatcher	*Muscicapa striata*	-3.211	0.624	Migrant	55	7.125	157	Insect	Woodland	17	28.5	vegetation	-0.01	64.4
Starling	*Sturnus vulgaris*	-2.645	0.412	Resident	54	5.25	109	Highly specialist	Farmland	77.5	34	hole	-	-
Stonechat	*Saxicola torquata*	19.766	2.477	Partial migrant	93	11.875	115	Highly specialist	Generalist	15	29.5	ground	-	-
Swallow	*Hirundo rustica*	2.904	0.511	Migrant	83	9	156	Invertebrate	Farmland	19	39	hole	-0.2	42.34
Treecreeper	*Certhia familiaris*	0.072	0.611	Resident	54	11.5	117	Highly specialist	Woodland	9.5	31	hole	-	-
Tree Pipit	*Anthus trivialis*	-1.439	1.111	Migrant	49	6	132	Highly specialist	Woodland	23.5	26.5	vegetation	-0.23	47.07
Tree Sparrow	*Passer montanus*	4.860	1.546	Resident	84	12.5	137	Small seed	Farmland	23.25	29	hole	-	-
Wheatear	*Oenanthe oenanthe*	-1.625	0.862	Migrant	48	8.25	131	Insect	Upland	23.5	30.5	Hole	-0.17	38.17
Whinchat	*Saxicola rubetra*	-3.687	0.864	Migrant	32	5	145	Invertebrate	Upland	16.5	27.5	ground	-0.11	34.84
Whitethroat	*Sylvia communis*	1.845	0.531	Migrant	62	6.375	142	Insect	Farmland	15	25.5	vegetation	-0.14	53.05
Willow Tit	*Poecile montanus*	-5.740	0.725	Resident	32	7.5	118	Highly specialist	Woodland	11.25	32.5	vegetation	-	-
Willow Warbler	*Phylloscopus trochilus*	-1.693	0.622	Migrant	40	6	132	Insect	Woodland	9.5	28	vegetation	-0.19	68.09
Wren	*Troglodytes troglodytes*	2.159	0.832	Resident	68	12.5	122	Invertebrate	Generalist	9.5	33.5	vegetation	-	-
Yellowhammer	*Emberiza citrinella*	-3.886	0.757	Resident	81	8	149	Small seed	Farmland	30.5	28	ground	-	-
Yellow Wagtail	*Motacilla flava*	-1.211	0.212	Migrant	57	7.875	144	Invertebrate	Generalist	17.5	28	ground	-0.06	40.98

Figure A.1. Cluster dendrogram for detailed diet data analysis. The approximate p-value (au) for each node is given in red and the boostrap probability (bp) in green. One can consider that clusters (edges) with high AU values (e.g. 95%) are strongly supported by data (Shimodaira, 2002). Figures in blue identify the 7 diet groups (DS): (1) Small seed eaters (some insects in summer); (2) Large seed eaters; (3) Insect (including spiders) eaters; (4) Invertebrate eaters; (5) generalist species; (6) generalist species also eating carrion; (7) highly specialise eater



Collinearity and univariate analysis

These tables present the Generalized Variance Inflation Factors (GVIF) (Table A.2 and A.3) and univariate analysis (Table S4) for the predictor pool used in the population trend analysis for UK passerine birds.

Table A.2 Generalized Variance Inflation Factor (GVIF) values for the candidate predictors of population trends for all UK passerines. GVIF^(1/2df) adjusts the GVIF values for the dimensions of the confidence ellipsoids.

Predictor	GVIF	Df	GVIF^(1/2df)
Average body weight	5.7	1	2.4
Average nesting period	14.7	1	3.8
Average clutch size	32.0	1	5.7
Average number of broods	95.2	1	9.8
Productivity	71.2	1	8.4
Average layind date	9.4	1	3.1
Average 1st clutch laying period	2.8	1	1.7
Migration strategy	31.1	2	2.4
Nesting location	8.9	2	1.7
Diet type	1373.5	6	1.8
Habitat preference	38.1	5	1.4

Table A.3. Results of correlation analysis for pairs of trait predictors suspected to hold similar biological information.

Predictor pairs	Pearson coefficient	t	df	P
Productivity, Average clutch size	0.35	2.55	48	0.014
Productivity, Number of brood per year	0.71	6.94	48	< 0.0001
Average clutch size, Number of brood per year	-0.38	-2.81	48	0.007
Average nesting period, Average body weight	0.85	11.39	48	< 0.0001
Diet type, Diet richness	0.01	2.40	48	0.02

Table A.4. Results of univariate analysis of the initial pool of predictors for all passerine species in the UK (shaded rows indicate predictors selected for the relative importance analysis and subsequent final model analysis).

	Unweighted model		Weighted model	
Predictor	F	P	F*	p*
Average laying date	5.01	0.03	6.02	0.02
Average 1st clutch laying period	3.41	0.07	0.40	0.53
Diet richness	2.04	0.16	0.20	0.65
Average body weight	2.82	0.09	0.76	0.39
Productivity	0.02	0.89	3.47	0.07
Average clutch size	0.001	0.97	1.14	0.29
Number of brood per year	3.04	0.09	0.28	0.60
Average nesting period	2.45	0.12	1.44	0.23
Migratory behaviour	1.62	0.21	1.30	0.28
Diet type	0.51	0.79	2.21	0.06
Nest location	1.04	0.36	0.19	0.83
Habitat	0.93	0.47	1.34	0.26

Impact of model weighting

Models reported in the main text were weighted by the standard error of the growth rate estimates. Here we present the model performance and coefficients for the unweighted models for all species and migrant species. The unweighted models contained fewer predictors and explained less variance in population trends than weighted models particularly for all passerines. Where predictors were common between weighted and unweighted models, the magnitude of coefficients were broadly similar. In contrast to weighted models however, the unweighted model residuals were not normal, further indicating the value of the weighting procedure in accounting for the errors in estimation of species growth rates.

Table A.5.Model performance and coefficients for the final unweighted model for all species.

Predictor	Coefficient (SE)	AIC_c	Adj D^2
Average laying date	-0.08(0.03)**	269.4	0.195
Average laying period	-0.07(0.02)**		

Table A.6 Model performance and coefficients for the final unweighted model for migrant species.

Predictor	Coefficient (SE)	AIC_c	Adj D^2
Average laying period	0.09(0.03)	54.25	0.754
Mean change in arrival date	10.88(3.37)		
Mean distance	-0.05(0.03)		

Phylogenetic analysis

Phylogenetic comparative methods are widely used to control for the lack of statistical independence among related species (Freckleton et al., 2002). A suite of comparative tests have been developed to deal with issues of non-independence, including phylogenetic generalized least squares (PGLS) (Pagel, 1997), where the expected covariance due to relatedness between species is included as an error matrix.

Pagel (1999) suggested a method to adjust analyses for varying levels of phylogenetic dependence by weighting the covariance matrix by λ (where λ=0 indicates no covariance and λ=1 indicates high covariance). Optimal *lambda* values can be estimated using a maximum likelihood approach. Martins (1996) argued that finding evidence for phylogenetic dependence of traits (equivalent to finding λ > 0) may be used to justify the need for phylogenetic analysis.

As described in the main text, PGLMs had higher AIC_c values than GLMS and estimated values of lambda were low and not significantly different from 0 (i.e. in both cases λ<0.001 with the test against λ=1 significantly different p<0.001 and the test against λ=0 non-significant p=1). PGLM

Table A.7. Comparison of model performance and characteristics between phylogenetic and non-phylogenetic models for (a) all species and (b) migrants.

(a) All species			(b) Migrants	
Model	**AIC_c**	**Λ**	**AIC_c**	**Λ**
Pglm.lam	332.01	0	68.32	0
Pglm.lam	334.62	1	68.32	1
Pglm.estimated	332.01	~0	68.89	~0
Non-phylo(no weights)	269.4	-	54.67	-
Non-phylo(weights)	271.5	-	53.41	-

Table A.8. Comparison of predictor coefficients between phylogenetic and non-phylogenetic models for all species.

Predictor (from final model)	Coefficient (SE) GLM no weights	Coefficient (SE) GLM weights	Coefficient (SE) PGLM (λ=0)	Coefficient (SE) GLM (λ=1)	Coefficient (SE) GLM (λ=opt)
Average body weight	-	0.005(0.004)	0.006(0.005)	0.006(0.004)	0.006(0.005)
Productivity	-	0.48(0.14)***	0.61(0.24)**	0.80(0.27)**	0.61(0.24)**
Average laying date	-0.08(0.03)**	-0.07(0.03)*	-0.04(0.05)*	-0.09(0.05)*	-0.04(0.05)*
Average laying period	0.07(0.02)**	-0.001(0.02)	-0.033(0.05)	-0.001(0.05)	-0.033(0.05)
Migration strategy(partial migrant) ¨	-	-2.26(2.24)	-1.68(5.19)	-2.2(4.7)	-1.68(5.19)
Migration strategy (migrant) ¨	-	-7.57(3.56)**	-0.33(6.01)	-6.2(7.47)	-0.33(6.01)
Habitat preference(Farmland)•	-	-1.5(1.03)	-3.19(2.06)	-1.98(2.04)	-3.19(2.06)
Habitat preference(Woodland)•	-	-0.84(1.03)	-3.38(1.74)*	-2.73(1.94)	-3.38(1.74)*
Habitat preference(Wetland)•	-	2.67(1.45)*	-1.13(2.46)	0.63(2.66)	-1.13(2.46)
Habitat preference(Urban)•	-	-1.12(1.05)	-3.43(2.06)	-2.49(1.88)	-3.43(2.06)
Habitat preference(Upland)•	-	0.26(1.56)	-2.87(2.7)	-3.94(2.61)	-2.87(2.7)
Diet type(large seeds) ˇ	-	2.64(1.06)**	-0.39(2.25)	-0.07(3.22)	-0.39(2.25)
Diet type(insects) ˇ	-	0.35(1.73)	-0.3(2.85)	1.58(2.92)	-0.3(2.85)
Diet type(invertebrates) ˇ	-	-1.87(1.32)	-2.37(2.29)	-2.74(2.51)	-2.37(2.29)
Diet type(generalist) ˇ	-	2.64(1.41)*	1.9(2.87)	2.63(2.96)	1.9(2.87)
Diet type(generalist + carrion) ˇ	-	0.17(1.95)	2.06(3.78)	0.42(5.03)	2.06(3.78)
Diet type(highly specialist) ˇ	-	-0.65(1.34)	1.42(2.46)	1.22(2.32)	1.42(2.46)
*Average laying period*Migration strategy(partial migrant)* ¨	-	0.02(0.03)	0.05(0.07)	0.04(0.06)	0.05(0.07)
*Average laying period*Migration strategy(migrant)* ¨	-	0.18(0.06)***	0.06(0.09)	0.15(0.11)	0.06(0.09)

Table A9. Comparison of predictor coefficients between phylogenetic and non-phylogenetic for migrant species.

Predictor	Coefficients(SE)				
Predictor (from final model)	**GLM no weights**	**GLM weights**	**PGLM (λ=0)**	**PGLM (λ=1)**	**PGLM (λ=opt)**
Mean change in arrival date	10.88(2.32)**	12.05(2.32)*	11.25.(3.78)*	12.06(3.99)*	11.35(3.78)*
Average 1st clutch laying period	0.09(0.03)**	0.13(0.03)*	0.11(0.04)*	0.11(0.04)*	0.11(0.04)*
Average laying date		0.08(0.04)	0.05(0.04)	0.03(0.05)	0.05(0.04)
Mean distance	-0.05(0.03)	-	-	-	-

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B. Supplementary information to Chapters 3 and 4

Table B.1 Species list with species' orders used in the community analysis

Species	Species code	Order
ARCTIC SKUA	AC	Charadriiformes
ARCTIC TERN	AE	Charadriiformes
LITTLE TERN	AF	Charadriiformes
SPOTTED CRAKE	AK	Gruiformes
CRANE	AN	Gruiformes
AVOCET	AV	Charadriiformes
BLACKBIRD	B.	Passeriformes
BAR-TAILED GODWIT	BA	Charadriiformes
BLACKCAP	BC	Passeriformes
BEAN GOOSE	BE	Anseriformes
BULLFINCH	BF	Passeriformes
BRENT GOOSE	BG	Anseriformes
BLACK-HEADED GULL	BH	Charadriiformes
BITTERN	BI	Ciconiiformes
BLACK TERN	BJ	Charadriiformes
BLACK GROUSE	BK	Galliformes
BRAMBLING	BL	Passeriformes
BLACK-NECKED GREBE	BN	Podicipediformes
BARN OWL	BO	Strigiformes
BEARDED TIT	BR	Passeriformes
BLUE TIT	BT	Passeriformes
BLUETHROAT	BU	Passeriformes
BLACK-THROATED DIVER	BV	Gaviiformes
BLACK-TAILED GODWIT	BW	Charadriiformes
BLACK REDSTART	BX	Passeriformes
BARNACLE GOOSE	BY	Anseriformes

BUZZARD	BZ	Accipitriformes
CARRION CROW	C.	Passeriformes
CORMORANT	CA	Pelecaniformes
CORN BUNTING	CB	Passeriformes
CHIFFCHAFF	CC	Passeriformes
COLLARED DOVE	CD	Columbiformes
CORNCRAKE	CE	Gruiformes
CHOUGH	CF	Passeriformes
CANADA GOOSE	CG	Anseriformes
CHAFFINCH	CH	Passeriformes
CRESTED TIT	CI	Passeriformes
CUCKOO	CK	Cuculiformes
CIRL BUNTING	CL	Passeriformes
COMMON GULL	CM	Charadriiformes
COMMON TERN	CN	Charadriiformes
COOT	CO	Gruiformes
CAPERCAILLIE	CP	Galliformes
COMMON CROSSBILL	CR	Passeriformes
COMMON SANDPIPER	CS	Charadriiformes
COAL TIT	CT	Passeriformes
CURLEW	CU	Charadriiformes
CETTI'S WARBLER	CW	Passeriformes
COMMON SCOTER	CX	Anseriformes
SCOTTISH CROSSBILL	CY	Passeriformes
CROSSBILL (SP UNCERTAIN)	CZ	Passeriformes
DUNNOCK	D.	Passeriformes
WOOD DUCK	DC	Anseriformes
DIPPER	DI	Passeriformes
DUNLIN	DN	Charadriiformes
DOTTEREL	DO	Charadriiformes

SPOTTED REDSHANK	DR	Charadriiformes
DARTFORD WARBLER	DW	Passeriformes
EIDER	E.	Anseriformes
GOLDEN EAGLE	EA	Accipitriformes
RED-BACKED SHRIKE	ED	Passeriformes
EGYPTIAN GOOSE	EG	Anseriformes
FULMAR	F.	Procellariiformes
FIRECREST	FC	Passeriformes
FIELDFARE	FF	Passeriformes
FERAL PIGEON / ROCK DOVE	FP	Columbiformes
GREEN WOODPECKER	G.	Piciformes
GADWALL	GA	Anseriformes
GREAT BLACK-BACKED GULL	GB	Charadriiformes
GOLDCREST	GC	Passeriformes
GOOSANDER	GD	Anseriformes
GREEN SANDPIPER	GE	Charadriiformes
GOLDEN PHEASANT	GF	Galliformes
GREAT CRESTED GREBE	GG	Podicipediformes
GRASSHOPPER WARBLER	GH	Passeriformes
GOSHAWK	GI	Accipitriformes
GREYLAG GOOSE	GJ	Anseriformes
GREENSHANK	GK	Charadriiformes
GREY WAGTAIL	GL	Passeriformes
GOLDENEYE	GN	Anseriformes
GOLDFINCH	GO	Passeriformes
GOLDEN PLOVER	GP	Charadriiformes
GREENFINCH	GR	Passeriformes
GREAT SPOTTED WOODPECKER	GS	Piciformes
GREAT TIT	GT	Passeriformes
GUILLEMOT	GU	Charadriiformes

GREY PLOVER	GV	Charadriiformes
GARDEN WARBLER	GW	Passeriformes
GANNET	GX	Pelecaniformes
GARGANEY	GY	Anseriformes
GLAUCOUS GULL	GZ	Charadriiformes
GREY HERON	H.	Ciconiiformes
HYBRID CROW	HB	Passeriformes
HOODED CROW	HC	Passeriformes
HAWFINCH	HF	Passeriformes
HERRING GULL	HG	Charadriiformes
HEN HARRIER	HH	Accipitriformes
HOUSE MARTIN	HM	Passeriformes
HOOPOE	HP	Coraciiformes
HOUSE SPARROW	HS	Passeriformes
HOBBY	HY	Accipitriformes
HONEY BUZZARD	HZ	Accipitriformes
ICTERINE WARBLER	IC	Passeriformes
RING-BILLED GULL	IN	Charadriiformes
JAY	J.	Passeriformes
JACKDAW	JD	Passeriformes
JACK SNIPE	JS	Charadriiformes
KESTREL	K.	Accipitriformes
KINGFISHER	KF	Coraciiformes
KITTIWAKE	KI	Charadriiformes
KNOT	KN	Charadriiformes
KENTISH PLOVER	KP	Charadriiformes
RED KITE	KT	Accipitriformes
LAPWING	L.	Charadriiformes
LESSER BLACK-BACKED GULL	LB	Charadriiformes
LONG-EARED OWL	LE	Strigiformes

LITTLE GREBE	LG	Podicipediformes
LINNET	LI	Passeriformes
LADY AMHERST'S PHEASANT	LM	Galliformes
LONG-TAILED DUCK	LN	Anseriformes
LITTLE OWL	LO	Strigiformes
LITTLE RINGED PLOVER	LP	Charadriiformes
LESSER REDPOLL	LR	Passeriformes
LESSER SPOTTED WOODPECKER	LS	Piciformes
LONG-TAILED TIT	LT	Passeriformes
LITTLE GULL	LU	Charadriiformes
LESSER WHITETHROAT	LW	Passeriformes
LITTLE STINT	LX	Charadriiformes
MISTLE THRUSH	M.	Passeriformes
MALLARD	MA	Anseriformes
MAGPIE	MG	Passeriformes
MOORHEN	MH	Gruiformes
MERLIN	ML	Accipitriformes
MANDARIN	MN	Anseriformes
MONTAGU'S HARRIER	MO	Accipitriformes
MEADOW PIPIT	MP	Passeriformes
MARSH HARRIER	MR	Accipitriformes
MUTE SWAN	MS	Anseriformes
MARSH TIT	MT	Passeriformes
MEDITERRANEAN GULL	MU	Charadriiformes
MARSH WARBLER	MW	Passeriformes
MANX SHEARWATER	MX	Procellariiformes
NIGHTINGALE	N.	Passeriformes
SPOONBILL	NB	Ciconiiformes
GREAT NORTHERN DIVER	ND	Gaviiformes
NUTHATCH	NH	Passeriformes

NIGHTJAR	NJ	Caprimulgiformes
RED-NECKED PHALAROPE	NK	Charadriiformes
SERIN	NS	Passeriformes
GREAT SKUA	NX	Charadriiformes
ORTOLAN BUNTING	OB	Passeriformes
OYSTERCATCHER	OC	Charadriiformes
WOOD SANDPIPER	OD	Charadriiformes
GOLDEN ORIOLE	OL	Passeriformes
OSPREY	OP	Accipitriformes
GREY PARTRIDGE	P.	Galliformes
PARROT CROSSBILL	PC	Passeriformes
PEREGRINE	PE	Accipitriformes
PIED FLYCATCHER	PF	Passeriformes
PINK-FOOTED GOOSE	PG	Anseriformes
PHEASANT	PH	Galliformes
PTARMIGAN	PM	Galliformes
POCHARD	PO	Anseriformes
PURPLE SANDPIPER	PS	Charadriiformes
PINTAIL	PT	Anseriformes
PUFFIN	PU	Charadriiformes
PIED WAGTAIL	PW	Passeriformes
QUAIL	Q.	Galliformes
ROBIN	R.	Passeriformes
RAZORBILL	RA	Charadriiformes
REED BUNTING	RB	Passeriformes
ROCK PIPIT	RC	Passeriformes
REDWING	RE	Passeriformes
ROUGH-LEGGED BUZZARD	RF	Accipitriformes
RED GROUSE	RG	Galliformes
RED-THROATED DIVER	RH	Gaviiformes

RING-NECKED PARAKEET	RI	Psittaciformes
REDSHANK	RK	Charadriiformes
RED-LEGGED PARTRIDGE	RL	Galliformes
RED-BREASTED MERGANSER	RM	Anseriformes
RAVEN	RN	Passeriformes
ROOK	RO	Passeriformes
RINGED PLOVER	RP	Charadriiformes
RED-CRESTED POCHARD	RQ	Anseriformes
ROSEATE TERN	RS	Charadriiformes
REDSTART	RT	Passeriformes
RUFF	RU	Charadriiformes
REED WARBLER	RW	Passeriformes
RED-NECKED GREBE	RX	Podicipediformes
RUDDY DUCK	RY	Anseriformes
RING OUZEL	RZ	Passeriformes
SKYLARK	S.	Passeriformes
SHAG	SA	Pelecaniformes
SNOW BUNTING	SB	Passeriformes
STONECHAT	SC	Passeriformes
STOCK DOVE	SD	Columbiformes
SHORT-EARED OWL	SE	Strigiformes
SPOTTED FLYCATCHER	SF	Passeriformes
STARLING	SG	Passeriformes
SPARROWHAWK	SH	Accipitriformes
SWIFT	SI	Apodiformes
SNOW GOOSE	SJ	Anseriformes
SISKIN	SK	Passeriformes
SWALLOW	SL	Passeriformes
SAND MARTIN	SM	Passeriformes
SNIPE	SN	Charadriiformes

SNOWY OWL	SO	Strigiformes
SCAUP	SP	Anseriformes
SCARLET ROSEFINCH	SQ	Passeriformes
SANDERLING	SS	Charadriiformes
SONG THRUSH	ST	Passeriformes
SHELDUCK	SU	Anseriformes
SHOVELER	SV	Anseriformes
SEDGE WARBLER	SW	Passeriformes
SMEW	SY	Anseriformes
SLAVONIAN GREBE	SZ	Podicipediformes
TEAL	T.	Anseriformes
TREECREEPER	TC	Passeriformes
TURTLE DOVE	TD	Columbiformes
SANDWICH TERN	TE	Charadriiformes
SHORT-TOED TREECREEPER	TH	Passeriformes
TEMMINCK'S STINT	TK	Charadriiformes
LEACH'S PETREL	TL	Procellariiformes
STORM PETREL	TM	Procellariiformes
STONE CURLEW	TN	Charadriiformes
TAWNY OWL	TO	Strigiformes
TREE PIPIT	TP	Passeriformes
TREE SPARROW	TS	Passeriformes
TURNSTONE	TT	Charadriiformes
TUFTED DUCK	TU	Anseriformes
TWITE	TW	Passeriformes
BLACK GUILLEMOT	TY	Charadriiformes
SAVI'S WARBLER	VI	Passeriformes
VELVET SCOTER	VS	Anseriformes
WHEATEAR	W.	Passeriformes
WATER RAIL	WA	Gruiformes

WHINCHAT	WC	Passeriformes
WHITE-TAILED EAGLE	WE	Accipitriformes
WHITE-FRONTED GOOSE	WG	Anseriformes
WHITETHROAT	WH	Passeriformes
WATER PIPIT	WI	Passeriformes
WOODCOCK	WK	Charadriiformes
WOODLARK	WL	Passeriformes
WHIMBREL	WM	Charadriiformes
WIGEON	WN	Anseriformes
WOOD WARBLER	WO	Passeriformes
WOODPIGEON	WP	Columbiformes
WREN	WR	Passeriformes
WHOOPER SWAN	WS	Anseriformes
WILLOW TIT	WT	Passeriformes
WILLOW WARBLER	WW	Passeriformes
WRYNECK	WY	Piciformes
YELLOWHAMMER	Y.	Passeriformes
YELLOW WAGTAIL	Y.W	Passeriformes

C. Supplementary information to Chapter 5

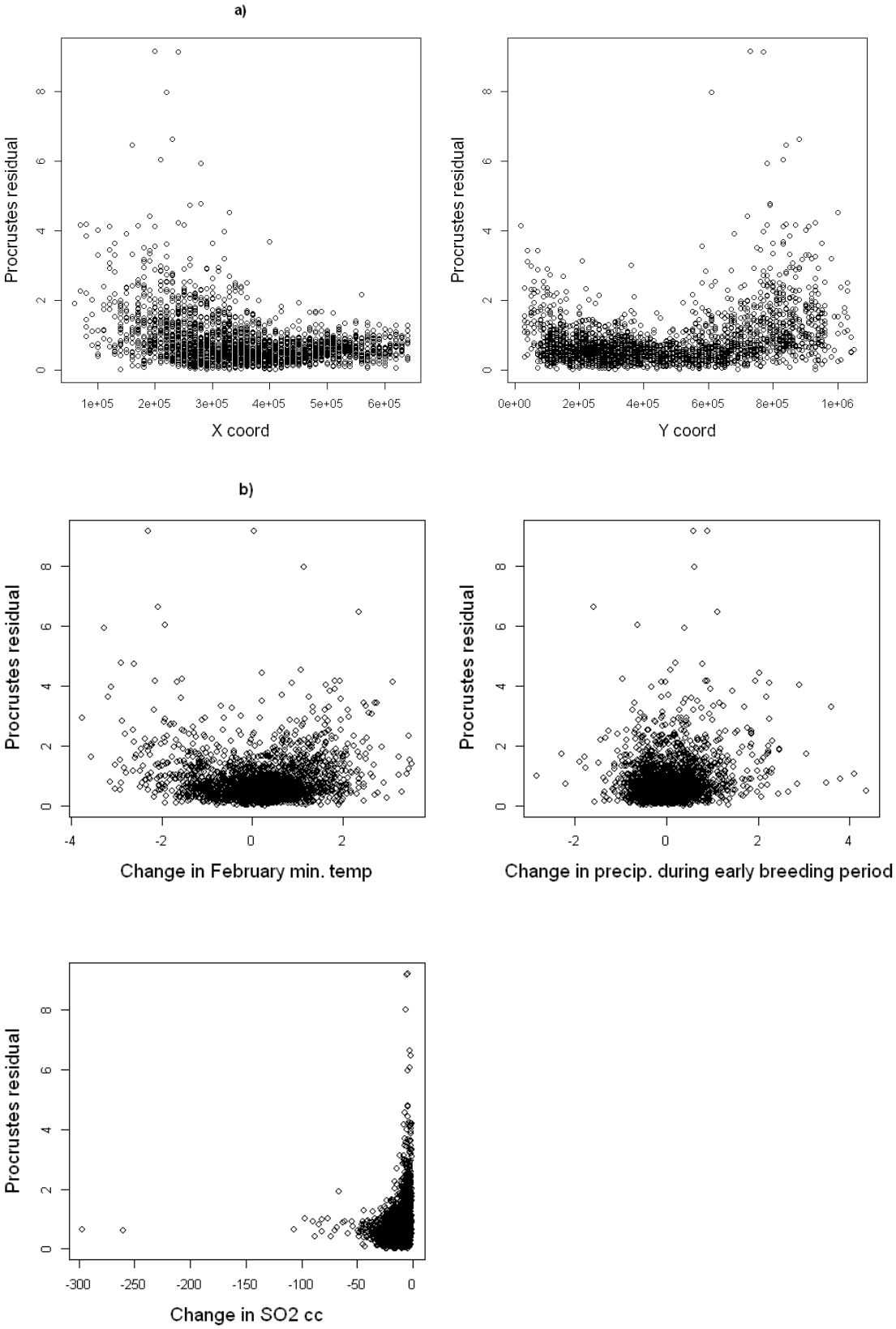

Figure B.2 Scatter plots of Procrustes species distances versus: a) sites geographical coordinates b) environmental variables used in the analysis. (The correlation coefficients for each variable are: r_x=-0.345, r_y=0.297, $r_{FebminT}$=0.009, r_{EBP}=0.152, r_{So2}=0.226)

D. Supplementary information to chapter 6

Table D.1. Predictors contribution to the final colonisation and extinction models

Colonisation model			Extinction model		
	AIC	**Change in AIC**		**AIC**	**Change in AIC**
overall BIC model	**18705**		**overall BIC model**	**63126**	
lambda_pt15	22609	3904	lambda_pt15	67470	4344
change predator number	19156	451	prevalence90	65627	2501
Migration behaviour: Change Feb min temperature	18877	172	Average laying date	63281	155
Farmland species	18768	63	Farmland species	63274	148
prevalence90	18741	36	Migration behaviour: Change Feb min temperature	63214	88
Average laying date: Change Feb min temperature	18740	35	Average 1st clutch laying period: Change Feb min temperature	63167	41
Average body weight	18737	32	Diet type: Feb min temperature	63157	31
Diet type: Change Feb min temperature	18734	29	Average brood number: Change Feb min temperature	63154	28
Average 1st clutch laying period: Feb min temperature	18730	25	Average 1st clutch laying period: Feb min temperature	63148	22
Average brood number : Change Feb min temperature	18724	19	Woodland species : change predator number	63141	15
Migration behaviour: Feb min temperature	18708	3	Average body weight	63137	11
main effects model	**18924**		**main effects model**	**63390**	
lambda_pt15	23333	4409	lambda_pt15	67947	4557
Change predator number	19375	451	prevalence90	65860	2470
Feb min temperature	19217	293	change predator number	65848	2458
Farmland species	19011	87	Feb min temperature	64330	940
Migration behaviour	18997	73	Migration behaviour	63554	164
Change Feb min temperature	18979	55	Average laying date	63548	158
prevalence90	18967	43	Farmland species	63541	151
Average 1st clutch laying period	18958	34	Woodland species	63501	111
Average brood number	18945	21	Average brood number	63405	15
Average body weight	18938	14	Average body weight	63397	7
Diet type	18935	11	Average 1st clutch laying period	63397	7
			Diet type	63392	2
			Change in Feb min temperature	63390	0

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